





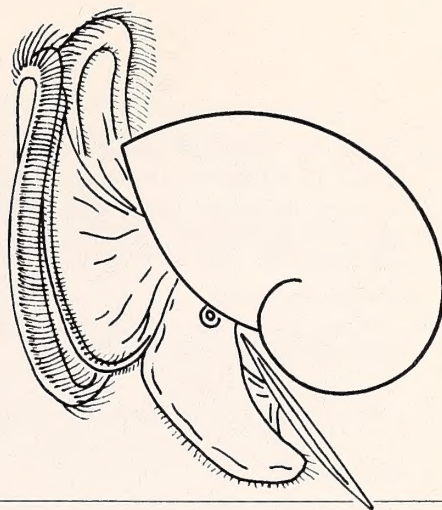




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THE VELIGER

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Volume 27

July 2, 1984 to April 1, 1985

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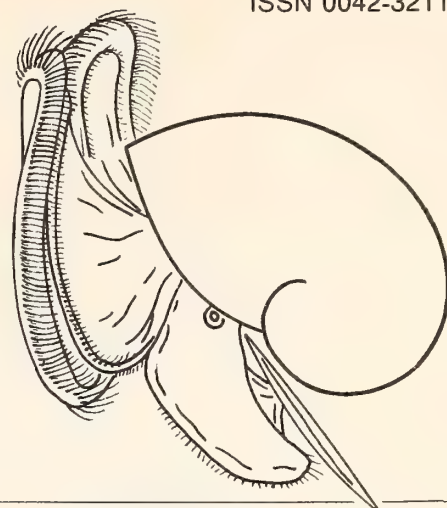
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THE VELIGER

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The Veliger is open to original papers pertaining to any problem concerned with mollusks.

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Send manuscripts, proofs, books for review, and correspondence regarding editorial matters to: Dr. David W. Phillips, Editor, 2410 Oakenshield Road, Davis, CA 95616 USA.

Aggregation in a Tropical Neritid

by

STEPHEN D. GARRITY

Department of Zoology, University of Massachusetts,
Amherst, Massachusetts 01003

AND

SALLY C. LEVINGS¹

Department of Zoology, University of Rhode Island,
Kingston, Rhode Island 02881

Abstract. Aggregation by the tropical intertidal mollusk *Nerita scabricosta* was examined. This behavior reduced mortality rates, especially for smaller snails. Habitat selection, size-specific differences in movement patterns, and the physical structure of the substratum were important in the formation and maintenance of aggregations.

INTRODUCTION

SNAILS of the genus *Nerita* (Archaeogastropoda) are common inhabitants of tropical hard-substratum shores. *Nerita scabricosta* (Lamarck, 1822) inhabits the upper levels of exposed rocky shores (GALTISOFF, 1950; HEDGPETH, 1969) from Baja California to Ecuador (KEEN, 1971).

In Panama, *Nerita scabricosta* (hereafter referred to as *Nerita*) exists in a harsh environment (GARRITY, 1984). Many shorelines throughout the world are covered by macroalgae and/or sessile invertebrates (LEWIS, 1964; STEPHENSON & STEPHENSON, 1972); these ameliorate physical conditions during low tides by shading the rock and/or retaining water, and can provide shelter to other organisms. The Pacific coast of Panama is barren of macroalgae (EARLE, 1972), and dense beds of mussels, barnacles, or oysters are rare (GARRITY & LEVINGS, 1981; MENGE & LUBCHENCO, 1981). Low tide temperatures on this tropical shore can exceed 50°C (GARRITY, 1984). Further, *Nerita* is more-or-less constantly exposed to terrestrial conditions—snails move downshore behind falling tides from resting positions above the high water mark, then move upshore ahead of rising tides (GARRITY & LEVINGS, 1981).

Some mechanisms mollusks use to lessen physical stress on this region's rocky shores have been examined (GARRITY, 1984). *Nerita scabricosta* avoids potentially lethal daytime conditions by (1) a limited, cyclic activity

period, (2) the selective use of microhabitat, and (3) evaporative cooling. Here we examine the occurrence, function, and formation of multilayered aggregations in *Nerita*, and show that this behavior enhances individual survival. Differential movement patterns among size classes and the structure of the preferred microhabitat result in a typical size layering within aggregations, with smaller, more vulnerable individuals located beneath larger snails.

METHODS

Occurrence and Numerical Composition of Aggregations

We sampled four sites along the Pacific coast of Panama (Uva, Chitre, Taboguilla, and Naos Islands) during the period October 1982 to April 1983. We chose sunny days, when snails were inactive. At each site, we laid a 100-m transect tape along the shore in the splash zone. We then walked along the tape. As snails were encountered, we recorded whether they were solitary or aggregated (in contact with conspecifics), and counted the number of snails in each aggregation. We recorded whether snails were in "exposed" (defined as sloping, horizontal, or vertical rock) or "protected" (defined as crevices and tidepools) microhabitats. Protected microhabitats remain cooler and/or wetter during daytime exposures (GARRITY, 1984, fig. 2, table 2). Because *Nerita* strongly prefers crevices and tidepools (GARRITY, 1984), this method under-sampled aggregations in exposed microhabitats. Transect lines were extended laterally and additional data taken in

¹ Address for reprint requests.

exposed microhabitats until sample sizes were equal to those from protected microhabitats.

Three-dimensional Size Structure

We examined the three-dimensional structure of four aggregations of varying size on Culebra, Naos, and Uva Islands during sunny days in 1979 and 1983. We dissected aggregations layer by layer, marking the dorsal surfaces of all visible snails with chalk, removing them, and then repeating this on each successive layer until all were collected. We measured the shell lengths of snails in each layer with Vernier calipers.

Water Holding Capacity

Nerita scabricosta holds water extraviscerally in its non-partitioned shell (VERMEIJ, 1978). Individuals lose water during the day; this evaporation cools tissues significantly (GARRITY, 1984). We tested the relationship between snail size and the amount of free water held by removing inactive individuals of various sizes from the rock on Naos Island on an early morning, falling tide and quickly placing each over a funnel inserted into a small, preweighed vial. Snails expelled water into the vials as they withdrew into their shells. The water in each vial was weighed and plotted against shell length.

Effects of the Number of Snails in an Aggregation

To test the hypothesis that stress decreases with increasing numbers of individuals per aggregation, we set out groups of 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 75, 100, 125, 150, 175, 200, and 300 freshly collected *Nerita* on a sloping surface on Uva Island (30 March 1983). Each group contained small, medium, and large individuals. Seawater was poured over each at the start of the experiment. This gave all snails access to extraviscerally water, and wetted the rock so all snails could move freely within each group. After 6 h (0900–1500) groups of snails were collected and placed in separate mesh containers in a 50-L cooler filled with seawater aboard the R/V *Benjamin*. Water was changed at frequent intervals. After 24 h we examined each group and counted surviving snails.

Effects of Snail Size

To test the effect of size on susceptibility to physical stress, we collected ~600 specimens of *Nerita* from Naos Island and divided them into three groups: small (2–6 mm shell length), medium (12–16 mm) and large (22–26 mm). We kept snails overnight in shaded, running seawater tanks at the Naos Marine Laboratory, and then for the next three days (7–9 March 1983) placed subsamples of each group, in spaced arrays, on flat rock in the high zone of Naos Island. To prevent movement out of the spaced arrays, snails were not watered initially (as above). After

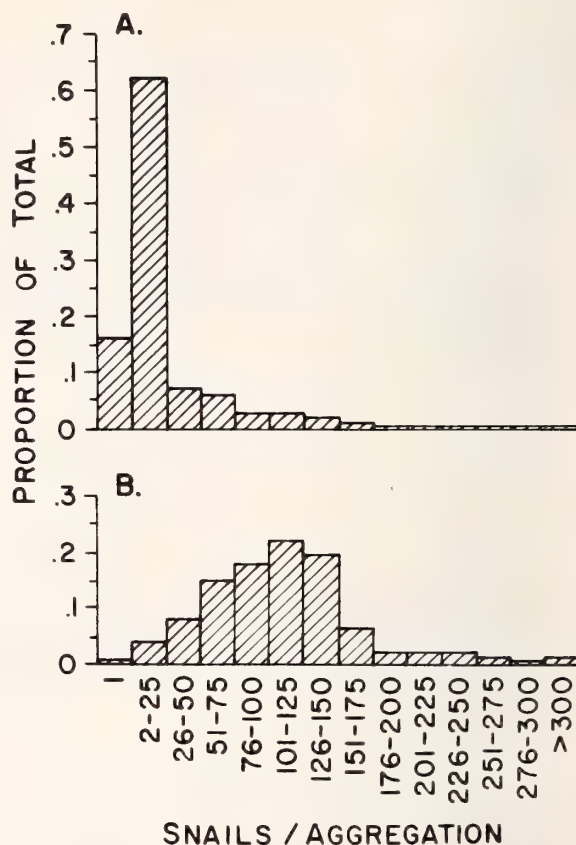


Figure 1

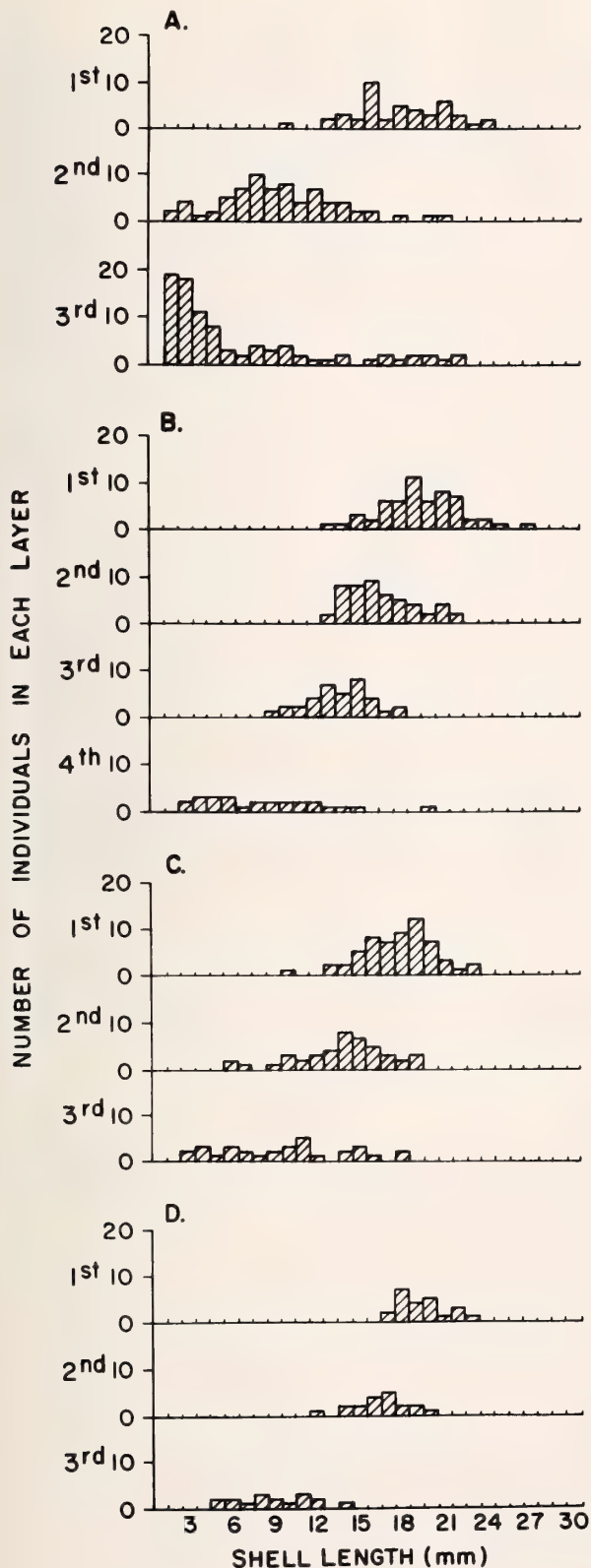
Distributions of aggregation sizes of *Nerita scabricosta*. Data are the proportions of different size classes of aggregations encountered in 800 aggregations sampled in (A) protected and 800 in (B) exposed microhabitats within a given range of number of snails. See text for further information.

6 h we collected them and placed each group in laboratory tanks. We counted the number of survivors after 24 h.

Formation of Aggregations

We observed the behavior of 50 previously marked (but otherwise undisturbed) small, medium, and large (see above section) snails in the field as they (1) became active on falling tides and left aggregations to graze, (2) foraged over wet or damp rock, and (3) became inactive either as the rock dried or as high tide approached. We recorded the number of snails that were active and the duration of activity, and looked for evidence of homing or trail-following behavior.

The role of substratum heterogeneity in the formation of aggregations was examined in April 1983 on Naos Island. We used four groups of ~200 snails (each group encompassing the natural size range of *Nerita*). Snails from each group were placed, as closely spaced but solitary individuals, on (1) a flat surface (exposed microhab-



itat), (2) a flat surface with several shallow depressions (semi-exposed), (3) a flat surface adjacent to a crevice (protected), and (4) a flat rock adjacent to a vertical surface (semi-protected). They were set out at the approximate high tide mark, on a rising tide just prior to the normal onset of activity, and examined for evidence of aggregation after 2 h (high tide), when movement had ceased.

RESULTS

We pooled data on the distribution of numbers of snails in aggregations of *Nerita*, because they did not differ among sites (Chi-square tests, $P > 0.1$). However, differences in the distribution of aggregation size classes between "exposed" and "protected" microhabitats were striking (Figure 1, Chi-square test, $P < 0.001$). Aggregations in crevices and tidepools had significantly fewer individuals (median number = 24) than those on vertical or flat rock (median number = 109, Mann-Whitney U test, $P < 0.001$). Snails aggregated in every microhabitat, but fewer than 1% occurred as solitary individuals ($n = 4$) on open surfaces compared to 16% ($n = 124$) in crevices and tidepools. It should be again noted that we did not sample all microhabitats with equal effort and are here comparing only the distribution of sizes of aggregations between exposed and protected microhabitats.

Dissections of aggregations in the field showed differences in snail size among layers (Figure 2). Larger individuals occurred primarily in the outer layers, and increasingly smaller snails formed the inner layers. This occurred over a range (59–209 snails) of aggregation sizes (Figure 2).

The amount of water held extraviscerally was positively related to snail shell length (Figure 3). These data best fit an exponential curve ($y = 0.01e^{0.18x}$, $r^2 = 0.90$, $n = 40$), indicating large snails hold proportionately more water than small ones (as expected from geometric considerations).

Both aggregation size and the size of individual snails were important in reducing physical stress. First, when groups containing different numbers of snails were set out on Uva Island for 6 h, there was a rough inverse relationship between mortality and aggregation size (Table 1, Spearman rank correlation coefficient = -0.97 , $P < 0.01$). Mortality was highest ($>80\%$) among snails in aggregations of ≤ 25 individuals. Mortality ranged from 17–73%

Figure 2

Sizes of *Nerita scabricosta* in the layers of aggregations. Data are the number of snails of a given size (shell length in mm) in each layer from four different aggregations. A. Aggregation on a vertical surface, $n = 209$, Uva. B. Aggregation from a crevice, $n = 170$, Culebra. C. Aggregation on a vertical surface, $n = 134$, Culebra. D. Aggregation from a small crevice, $n = 59$, Naos.

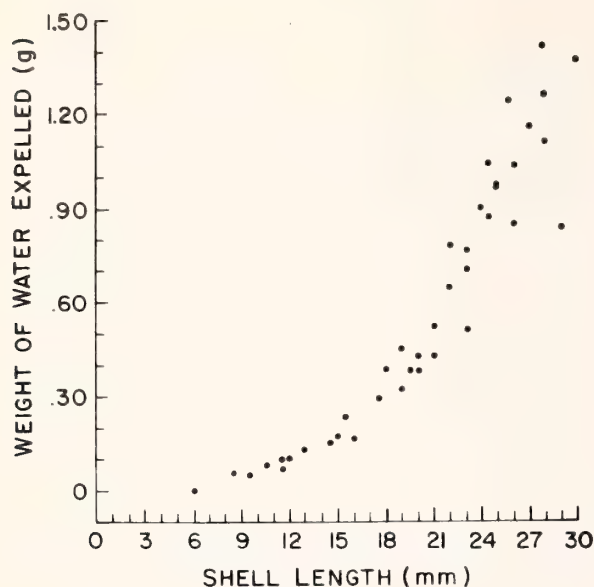


Figure 3

Amount of water held within the shell *vs.* shell length. Regression equation is: $y = 0.01e^{0.18x}$, $r^2 = 0.90$. See text for further explanation.

in aggregations of up to 100 snails. Only groups of 125 or more experienced less than 10% mortality, and there were two deaths in the largest ($n = 300$) group. Second, snails set out as solitary individuals on Naos Island showed size-dependent differences in mortality rates (Table 2).

Table 1

Mortality of *Nerita scabricosta* in artificially constructed clumps. Clumps were constructed on Uva Island and set out for 6 h during low tide. Snails were placed in mesh containers in frequently-changed seawater and survivors counted after 24 h.

Aggregation size	Number dead	Percent mortality after 24 h
5	4	80
10	9	90
15	13	87
20	17	85
25	21	84
30	22	73
35	19	54
40	18	45
45	20	44
50	23	46
75	22	29
100	17	17
125	8	6
150	6	4
175	3	2
200	4	2
300	2	1

Table 2

Mortality of spaced *Nerita scabricosta*. Snails were placed in spaced arrays on flat rocks for 6 h during low tide. They were then placed in running, shaded seawater and survivors counted after 24 h.

	Large (22–26 mm)		Medium (12–16 mm)		Small (2–6 mm)	
	N tested	N died	N tested	N died	N tested	N died
Day 1	46	4	51	34	55	51
Day 2	75	5	75	29	75	58
Day 3	75	7	75	51	75	70
Total	196	16	201	114	205	183
Proportion dead		.08		.57		.89

Snails died in all size classes, but significantly fewer large snails died than medium ones (8% *vs.* 57% overall, Chi-square test, $P < 0.001$), and significantly fewer medium-sized snails died than small *Nerita* (57% *vs.* 89% overall, Chi-square test, $P < 0.001$). Some mortality in these experiments may have resulted from handling; however, all snails were handled in the same way. High rates of mortality do not reflect events in nature. Snails were set out in flat or sloping homogeneous rock (very exposed micro-habitat) to facilitate comparisons among treatments.

Observations of marked individuals in the field showed shell size was an important variable in patterns of movement (Table 3). During the tidal cycle, more large snails

Table 3

Movement patterns for differently-sized *Nerita scabricosta*.

A. Percent movement.¹

Snail size	Time						
	High tide	+2 h	+4 h	Low tide	+8 h	+10 h	High tide
Small	0	11	0	0	0	8	0
Medium	0	47	12	3	1	16	0
Large	0	64	35	9	14	51	1

B. Distance moved.²

Snail size	Median	Range	Probability
Small	0.1 m	0.03–0.48	<0.001
Medium	1.3 m	0.06–4.14	<0.001
Large	3.62 m	0.05–6.70	

¹ Percent of 50 snails in each size class active at a given time over a complete tidal cycle (12 h). Small snails = 2–6 mm, medium snails = 12–16 mm, large snails = 22–26 mm.

² Distance moved from resting position, measured as outward path for the same snails as in (A); size classes as in (A). Probabilities are from comparisons of the distance moved by small and medium, and medium and large snails, using Mann-Whitney U tests.

became active than medium snails (Sign test, $P = 0.031$) and more medium snails were active than small ones ($P = 0.016$). A similar gradient appeared in the distances that differently sized, active individuals moved (Table 3B); the median distance moved by large snails (3.6 m) was significantly greater than that by medium snails (1.3 m), and the latter was significantly greater than for small snails (0.1 m, Mann-Whitney U tests, $P < 0.001$, both cases).

Snails of all sizes moved as the tide fell, but small snails were active for <0.5 h and moved back into crevices and aggregations as the rock dried. Seventeen of 50 medium and 38 of 50 large individuals moved downshore with the tide, rather than moving back. Larger snails sometimes followed visible trails left by conspecifics when moving up or downshore ($n = 23/108$), but seldom did so when grazing at lower levels ($n = 5/87$). Individuals did not always move back to the same aggregation or position. Over a five-day period, 33 of 50 large, marked snails dispersed to several other aggregations within 5 m of the original one. Net lateral movement along the shore is usually slow, except in the presence of the predaceous gastropod *Purpura pansa* (GARRITY & LEVINGS, 1981).

The nature of the substratum plays a role in the formation and structure of aggregations. Of the specimens of *Nerita* ($n = 200$) placed upon a flat, homogeneous surface, 127 remained solitary, and all aggregations had a single layer. The second group of 200 clustered around depressions present on the rock; again there were no multilayered groups and 58 snails remained solitary. Snails placed adjacent to a crevice all ($n = 201$) moved into it. Within the crevice, 26 were solitary and the rest in multilayered aggregations. Finally, *Nerita* placed adjacent to a vertical surface moved either to the angle formed by the intersection of the two surfaces where they formed a large ($n = 185$), multilayered aggregation, or onto the vertical surface ($n = 12$ aggregated in a single layer, 3 solitary).

DISCUSSION

Aggregation in limpets (review in BRANCH, 1981) and other herbivorous gastropods (ROHDE & SANDLAND, 1975; VANNINI & CHELAZZI, 1978, and included references) has been related to abiotic factors such as desiccation, wave action, or insolation, although the causes of this behavior have not been shown. Considerable evidence supports the notion that aggregation is an important mechanism to reduce physical stress in *Nerita scabricosta*. First, in natural situations, both the occurrence of snails in aggregations and the number of individuals per group were greatest in harsher microhabitats (Figure 1). Even in more benign microhabitats, the majority (84%) aggregated. Mean tissue temperatures of snails in aggregations stay significantly lower than those of solitary ones throughout the day, both on open rock and in crevices (GARRITY, 1984, fig. 11), and the mortality rate of aggregated snails is lower than that of solitary ones (GARRITY, 1984, table 5). Field manipulations of aggregation size in an exposed mi-

crohabitat showed members of larger groups survived better than *Nerita* in small ones (Table 1).

Most aggregations consisted of two or more layers and had a distinct size structure; larger individuals occurred chiefly in the top layer and the proportion of smaller snails increased with depth (Figure 2). The smallest size classes were never represented in the top layer. This size structure may have chiefly benefited small *Nerita*, because they held proportionately less water (Figure 3) and were most vulnerable to stress (Table 2). Snails in the interior of aggregations were both shaded and dampened by those above; it also is likely, given the movement pattern of small *Nerita* (Table 3B), that water trickled by larger snails in aggregations was a source of extravisceral water for small ones in bottom layers. Although water lost by solitary snails decreases with size, larger individuals in aggregations lose proportionately more water than small ones (GARRITY, 1984, fig. 12).

The formation and maintenance of aggregations had several components. Perhaps most importantly, *Nerita* chose crevices and tidepools, comprising $<20\%$ of the rock surface in the splash zone (GARRITY, 1984, fig. 1), and avoided more exposed areas of the rock during periods of inactivity (LEVINGS & GARRITY, 1983, table 3). This behavior gave inactive *Nerita* a clumped distribution in space. Second, size-specific activity patterns tended to maintain aggregations and could result in snails being layered by size: small individuals moved short distances and were active only briefly before returning to aggregation sites (Table 3). As shell size increased, so did foraging time and distance (Table 3; also see LEVINGS & GARRITY, 1983, fig. 2). Larger snails moved into aggregations last, and thus occurred in the outer layers. The nature of the substratum may enhance this effect. Crevices, the most preferred microhabitat, are wider at the mouth than at the bottom. Larger snails were thus excluded from bottom layers (see also RAFFAELLI & HUGHES, 1978). Small crevices, pocks, or depressions are probably foci for aggregations found on horizontal or sloping surfaces. The occurrence of these microsites in nature was not monitored in our transects. However, when groups of 200 spaced snails were placed (a) on flat, homogeneous rock and (b) on a flat surface containing several small depressions, more of the second group aggregated, and aggregations centered on the depressions. Lastly, larger *Nerita* moved up- and downshore as a wave front immediately behind falling tides and ahead of rising tides (GARRITY & LEVINGS, 1981). During this vertical movement, individuals frequently followed slime trails of leading snails. These two behaviors resulted in a clumped distribution when *Nerita* moved to or from refugia.

Nerita scabricosta actively avoids submergence. This reduces exposure to predaceous fishes (BERTNESS *et al.*, 1981), but results in increased exposure to potentially lethal conditions during the day. Behavioral mechanisms used by *Nerita* to reduce desiccation and thermal stress include a reduced activity period, microhabitat selection, and evap-

orative cooling. These mechanisms are enhanced by the formation of multilayered aggregations of up to several hundred snails, resulting from size-specific differences in behavior and activity patterns, and by the physical structure of preferred microhabitats. Aggregation is an important mechanism, especially for smaller *Nerita*, for the reduction of stress on this harsh tropical shore.

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Establishment of Mussel Beds: Attachment Behavior and Distribution of Recently Settled Mussels (*Mytilus californianus*)

by

JAMES H. PETERSEN¹

Department of Biology, University of Oregon,
Eugene, Oregon 97403

Abstract. The distribution and behavior of small *Mytilus californianus* (plantigrades) were studied, and results were interpreted with respect to intertidal community structure and establishment of mussel beds. *Mytilus californianus* plantigrades were found on mussel beds, algae, and bare rock. Highest densities of plantigrades were observed on the red alga *Endocladia muricata*. Field experiments and sample data suggest that algae that grow upon adult mussel shells have no effect on the density of settlers or plantigrades in a patch of mussels. Plantigrades were abundant in established mussel beds throughout the year because settlement is continuous. Laboratory choice experiments indicate *M. californianus* plantigrades do not select particular species for byssal attachment. *Mytilus californianus* beds are established only after a surface has been previously colonized. By settling and surviving upon many different surfaces, *M. californianus* is capable of establishing populations throughout a broad geographic range.

INTRODUCTION

PAST ECOLOGICAL work on the marine mussel *Mytilus californianus* Conrad, 1837, has emphasized population regulation (PAINE, 1966, 1974; ACKERMAN, 1971), competition with other sessile species (PAINE, 1966, 1974; HARGER, 1968, 1970a, b, 1972a, b; SUCHANEK, 1981), infaunal communities (HEWATT, 1935; KANTER, 1977; SUCHANEK, 1979), and the role of mussel beds in community structure (LEVIN & PAINE, 1974; PAINE & LEVIN, 1981). These studies have demonstrated that *M. californianus* is an important species in the intertidal community because of the competitive ability, persistence, and abundance of individuals and populations (mussel beds). However, relatively little work has been done on the attachment preferences and survival patterns of small *M. californianus*. Because adult distribution and abundance patterns are the result of small mussel behavior and survivorship, work on these topics should improve our understanding of intertidal community dynamics and population development of *M. californianus*.

PETRAITIS (1978) compared the distributions of juvenile

Mytilus californianus and *M. edulis* Linnaeus, 1758, in southern California and concluded that juveniles were more likely to be associated with conspecific adults than adults of the other species. He attributed these distributions to selective settlement (primary settlement) rather than movement of plantigrades (secondary settlement) or juvenile mortality. PAINE (1974) sampled algae, barnacles, and mussel beds in Washington and noted high densities of small mussels (less than 1.5 cm) among "filamentous" algae and the byssal threads of adult mussels.

This study presents data on the behavior and distribution of small, post-settlement *Mytilus californianus*. Specific emphasis is given to the distribution, abundance, and attachment behavior of plantigrades (individuals between 1.0 and 10.0 mm in length). Observed patterns are interpreted with respect to mussel bed establishment and local community structure. Data on primary settlement patterns and pediveliger behavior of *M. californianus* are presented elsewhere (PETERSEN, 1984).

DISTRIBUTION AND DENSITY OF PLANTIGRADES

The major study site was Mussel Reef on Yoakam Point, Oregon (43°20'N; 124°22'W). Mussel Reef is a flat, wave-cut platform about 2.0 m above mean lower low water.

¹ Present address: Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007.

Table 1

Density of *Mytilus californianus* plantigrades on various substrata at Mussel Reef, Oregon. Mean number of plantigrades is given per 100 cm² of substratum. Samples were collected in May and June of 1980.

Substratum	Mean	SD	n
<i>Endocladia muricata</i>	260.0	174.5	10
<i>Gigartina papillata</i>	125.0	128.8	5
<i>Cladophora</i> sp.	95.8	137.0	18
<i>Corallina vancouverensis</i> Yendo, 1902	79.3	82.8	6
<i>Rhodomela larix</i>	62.4	37.6	8
<i>Analphus japonicus</i> (Harvey) Wynne, 1971	40.0	33.5	5
Unclassified red alga #1	27.0	29.0	12
<i>Mytilus californianus</i>	21.6	9.1	8
<i>Polysiphonia</i> sp.	10.3	18.3	22
Bare-barnacle	0.0	0.0	9

Mussel beds of *Mytilus californianus* and patches of the red alga *Rhodomela larix* (Turner) C. Agardh, 1822, cover most of this sandstone platform (PETERSEN, 1983).

The abundance of plantigrades on several substrata was estimated at Mussel Reef. Pseudo-random points were established by blindly throwing an object onto mussel beds, algal dominated areas, or "bare-barnacle" patches. Bare rock areas usually included many small barnacles (primarily *Balanus glandula* Darwin, 1854, and *Chthamalus dalli* Pilsbry, 1916) so this substratum will be referred to as bare-barnacle. Samples were collected at a pseudo-random point, or as near one of these points as possible. *Mytilus californianus* beds were sampled by collecting all mussels, infauna, and sediment in a 100-cm² area. *Rhodomela larix* (25-cm² samples) and other substrata (4-cm² samples) were sampled by scraping all material in the given area into a plastic bag. Samples were returned to the laboratory and visually or mechanically sorted (PETERSEN, 1983). All mussels less than 10 mm in length were measured to the nearest 0.1 mm with an ocular micrometer; larger mussels were measured with vernier calipers.

Small *Mytilus edulis*, which were occasionally found at the study site (PETERSEN, 1983), and *M. californianus* are morphologically similar, and separation of plantigrades of these species is difficult (SUCHANEK, 1978; personal observation). To develop an identification criterion, *M. edulis* collected in Coos Bay, Oregon, and Spanish Ship Bay, Nova Scotia (supplied by Dr. Gary Newkirk), were compared with *M. californianus* of similar size from Mussel Reef. Individuals greater than 1.0 mm in length differed in the shape of the ventral shell margin immediately posterior to the umbo. The ventral margin of *M. edulis* valves is straight or slightly convex from the umbo to the posterior part of the shell where the margin bends dorsally. However, the ventral shell margin of *M. californianus*

Table 2

Mean percent cover on shells of *Mytilus californianus* from established mussel beds at Mussel Reef, Oregon. Samples (n = 74) were collected between June 1979 and September 1981.

Substratum	Mean (%)	SD
Bare shell	86.8	7.2
Barnacles	8.8	5.7
<i>Cladophora</i> sp.	1.3	3.6
<i>Polysiphonia</i> sp.	1.1	2.4
<i>Rhodomela larix</i>	0.7	2.9
<i>Endocladia muricata</i>	0.4	1.5
<i>Fucus distichus</i> Linnaeus, 1767	0.3	1.6
<i>Spirorbis borealis</i> Daudin, 1800	0.2	0.5
<i>Anthopleura elegantissima</i> (Brandt, 1835)	0.1	0.3
<i>Corallina vancouverensis</i>	0.1	0.4
<i>Odonthallia floccosa</i> (Esper)		
Falkenberg, 1901	0.1	0.5
<i>Haliclona</i> sp.	0.1	0.5
<i>Gigartina papillata</i>	<0.1	
<i>Ulva lactuca</i> Linnaeus, 1753	<0.1	
<i>Gelidium</i> sp.	<0.1	
<i>Halichondria</i> sp.	<0.1	
All algae	3.9	7.4

plantigrades usually has a small, gentle indentation immediately posterior to the umbo region. Identification of plantigrades was based upon this characteristic of the shell. Mussels less than 1.0 mm in length could not be easily identified to species, so these individuals are referred to as "settlers."

Small mussels were found on all substrata sampled, except the bare-barnacle surface (Table 1). Density was highest on the red alga *Endocladia muricata* (Postels & Ruprecht) J. Agardh, 1847, with 260.0 plantigrades/100 cm² of alga. Other algae had plantigrade densities between 125.0/100 cm² on *Gigartina papillata* (C. Agardh) J. Agardh, 1846, and 10.3/100 cm² on *Polysiphonia* sp. The density of plantigrades in *Mytilus californianus* beds (21.6 plantigrades/100 cm²) was relatively low compared to other substrata sampled.

The high variability of these data probably indicates a true patchy distribution of plantigrades and not just a sampling problem. All algal and bare-barnacle samples, except *Rhodomela larix*, were 4 cm². Because many of the algae sampled occur as small patches, increasing sample size to improve the estimates was not possible. Moreover, the data from *R. larix* samples were also highly variable, although sample size was 25 cm² for this species. Increasing the number of samples of a substratum did not seem to improve the estimates; for example, the variation in *Polysiphonia* sp. (n = 22; coefficient of variation = 178%) was greater than for those substrata where fewer samples were taken.

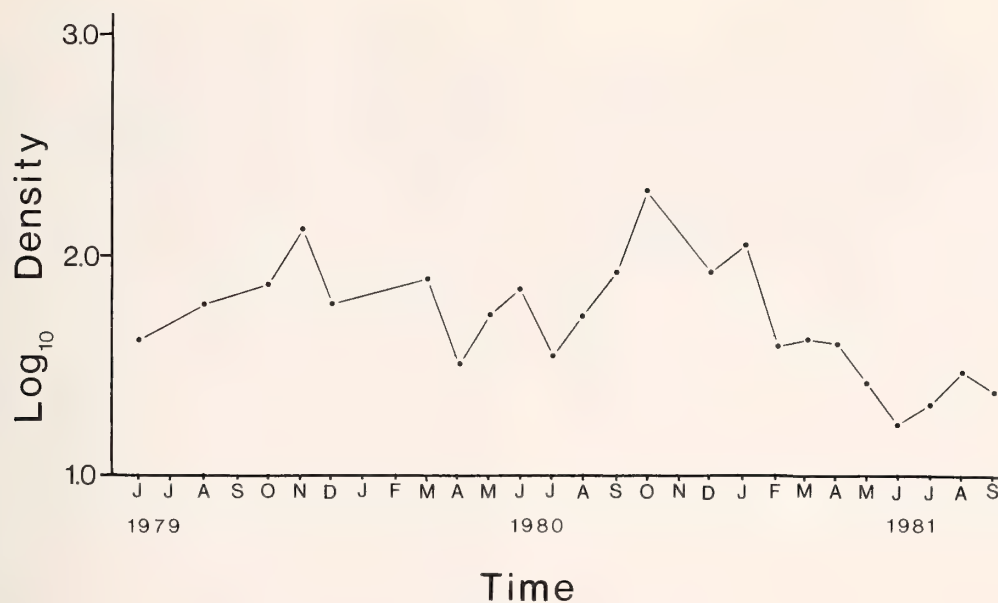


Figure 1

Density of *Mytilus californianus* plantigrades in *M. californianus* beds at Mussel Reef, Oregon. Each point is the mean number of plantigrades per 100 cm² of substratum. Most means are the average of four samples.

Plantigrades of *M. californianus* were present in established mussel beds throughout the sampling period (Figure 1). Plantigrade density in *M. californianus* samples followed roughly the same seasonal pattern as settlement density (PETERSEN, 1984): high numbers of settlers and plantigrades in late summer through fall and lower numbers during other parts of the year. Plantigrade density increased in the fall of 1980, corresponding to heavy larval settlement beginning in June 1980 and peaking in August 1980 (PETERSEN, 1984; see also KELLEY *et al.*, 1982). These summer settlers likely grew into the plantigrade category by fall, causing the increase shown in Figure 1.

ROLE OF ALGAE ON ADULT MUSSEL SHELLS

Several species of algae occur on mussel shells from the central Oregon coast (Table 2). The average cover of algae in all samples was about 4%, whereas the maximum cover was 30% in a sample collected in October 1980. The variation in total algal cover between samples was large because species were patchily distributed over the reef; some areas had a relatively heavy cover of algae and barnacles while in other areas the mussel shells were quite bare. SUCHANEK (1979) investigated the role of herbivores in mussel beds. When grazers (limpets and littorines, primarily) were removed from a patch of mussels, the percent cover of algae increased dramatically. Many herbivores were found in the samples collected at Mussel Reef, and they may be controlling the overall abundance of algae. These grazers may also be responsible for the patchy dis-

tribution of algal species on the mussel beds, if the density of herbivores is uneven across the reef. There were no obvious seasonal patterns in total algal abundance on mussel shells; however, annual species of algae were more abundant at certain times of the year, especially during the spring and summer.

Algae on shells in established mussel beds could affect the recruitment of settlers and plantigrades into the bed in several ways. As a settling larva swims and drifts through the water, it may encounter an algal thallus and begin testing this thallus or the nearby surfaces for their attachment suitability. The larva might attach to the alga itself or it might use the alga as a track to crawl to a more suitable substratum. Algal patches also increase the total exposed surface area of a mussel bed, thus increasing the chance that planktonic larvae will encounter a surface and settle in this area. If the alga has erect thalli, they may function as a net, filtering water moved by waves, tides, and currents.

To test the hypothesis that algae or barnacles on mussels increase larval settlement, or recruitment of plantigrades in the mussel bed, a removal experiment was carried out at Mussel Reef. In March 1980, five 400-cm² areas were haphazardly selected within the established mussel bed. In each of the five patches, at least 10% of the exposed shell was initially covered by algae. All of the algae and barnacles were scraped from the mussels in each area with a putty knife and a wire brush (Removal treatment). These five sites were scraped monthly to remove any algae or barnacles that settled on the mussel shells. After 12 months, 100-cm² samples were collected from the

Table 3

Density of settlers and *Mytilus californianus* plantigrades in algal removal experiments. Mean number of individuals, with SD, is given per 100 cm² of substratum. All data were collected in April 1981. Only those settlers and plantigrades that were attached by byssal threads to adult mussels were included in calculating these means; unattached and algal attached mussels were not included because this is a test of recruitment into the mussel matrix.

See text for an explanation of controls.

Treatment	Mean	SD	n	F
Settlers				
Removal	6.5	5.0	4	0.17 NS
High % algae control	4.5	6.4	2	
Low % algae control	5.0	2.8	2	
<i>Mytilus californianus</i> plantigrades				
Removal	38.5	21.9	4	0.60 NS
High % algae control	32.5	38.9	2	
Low % algae control	14.0	12.7	2	

NS = Not significant.

center of each 400-cm² removal area. One of the five original sites was damaged by winter waves, so only four samples of scraped mussels were collected. Two types of control samples were collected at the same time as the Removal samples: (1) samples that had more than 10% algal cover on the mussel shells (High % Algae Control), and (2) samples that had less than 1% algal cover on the mussels (Low % Algae Control). All samples were returned to the laboratory and processed in the usual fashion.

Data from the algal removal experiments suggest that settlement and plantigrade recruitment were not significantly affected by algae on adult mussel shells (Table 3). Settler densities were similar in all treatments and were not significantly different. Densities of plantigrades ranged from 38.5/100 cm² in the Removal treatment to 14.0/100 cm² in the Low % Algae Control; there was no statistical difference between treatments. Because variation in both controls and removals was high, a "significant" decrease in the removal series may have been difficult to detect. The relatively high densities of settlers and plantigrades in the Removal treatment, however, suggest there was no effect of removing algae from the adult shells.

Mussel samples collected between June 1980 and January 1981 were also used to test the effects of algal cover. During this period, settlement intensity was fairly constant at Mussel Reef (PETERSEN, 1984). The number of settlers in a sample was not related to the total percent algal cover in that sample ($P > 0.05$, $r^2 = 0.26$, $n = 22$). Also, the number of *Mytilus californianus* plantigrades and the total percent algal cover were unrelated ($P > 0.10$, $r^2 = 0.09$, $n = 22$). This correlative evidence and the removal experiment suggest that the presence of algae on

Table 4

Results of four-way choice experiments with *Mytilus californianus* plantigrades. E is the expected number of plantigrades attached to a substratum based on the encounter rate for that substratum. O is the observed number of attached plantigrades.

Substratum	Bound- ary (mm)	O	E	χ^2
Trial #1				
<i>M. californianus</i>	384	14	16.9	11.2*
<i>M. edulis</i>	425	28	18.7	
<i>Rhodomela larix</i>	427	8	18.8	
Sandstone	331	19	14.6	
Trial #2				
<i>M. californianus</i>	403	22	17.8	8.5*
<i>M. edulis</i>	431	14	19.0	
<i>Rhodomela larix</i>	384	25	16.9	
Sandstone	323	7	14.3	

* = $P < 0.05$.

adult mussels does not significantly increase (or decrease) settlement or recruitment into the mussel bed.

PLANTIGRADE SELECTION EXPERIMENTS

The attachment preferences of *Mytilus californianus* plantigrades were investigated in the laboratory with four-way and two-way choice experiments. The four-way choice experiments were run in 30 × 60 cm glass aquaria. *Mytilus californianus* adults, *M. edulis* adults, *Rhodomela larix* thalli, and pieces of bare sandstone were the substrata tested. To make the encounter probabilities of the substrata approximately equal, and to avoid confounding effects of aquarium edges, each substratum was placed in a separate corner of the aquarium, and the inner boundary of a substratum was extended from the midpoint of one side of the aquarium to the midpoint of the adjacent side. This arrangement produced in the aquarium a diamond-shaped arena, the sides of which were the four test substrata. A searching plantigrade in this arena would encounter only the four test substrata and none of the aquarium edges. The expected encounter rate of a substratum was estimated by tracing the boundary of the substratum on paper, measuring the length of this boundary with an opisometer (a map distance-measurement instrument), and calculating what proportion of the total boundary length was attributable to this substratum.

All test substrata and plantigrades were collected from Mussel Reef. Mussels, algae, and sandstone were rinsed, and all animals and algae were removed using a dissecting microscope. Test substrata were placed in an aquarium, water was added, and the setup was left for 24 h before 100 naive *Mytilus californianus* plantigrades were haphaz-

ardly placed in the central arena. Plantigrades were allowed to search and attach for 24 h, after which the substrata were collected and the number of attached plantigrades was determined. During the search period, aquaria were kept in dim, diffuse light and aeration was provided. Two trials of these four-way choice experiments were run.

Table 4 lists the data and analyses of the four-way choice experiments. In the first trial, of those plantigrades that chose a substratum, *Mytilus edulis* adults were preferred (40.6% of all attached individuals). Only eight plantigrades chose *Rhodomela larix* thalli, much less than the 18.8 expected based upon the encounter probabilities. The number of plantigrades attached to sandstone and *M. californianus* were near the expected values. The results of the second trial differed somewhat from the first trial. *Rhodomela larix* was the preferred substratum (36.8% of all attached individuals) and sandstone was least preferred (10.3%). In both experiments, about one-third of the plantigrades tested were found unattached or attached to the glass in the central arena. Although both trials differed significantly from random attachment based upon the calculated encounter probabilities, the different results in the two trials and the high proportion of glass-attached individuals suggest that *M. californianus* plantigrades may not "prefer" any of these substrata over others.

Different results in the four-way experiments could also result from inadequate control of experimental factors; therefore, a second plantigrade attachment experiment was run. *Mytilus edulis*, *M. californianus*, and *Rhodomela larix* were used as test substrata in two-way choice experiments (Table 5). Each test substratum was distributed in a semi-circle around the edge of a 2-L finger bowl, and 30 plantigrades were added to the central area of the bowl. Plantigrades were allowed to search and attach for 12 h before the substrata were removed and examined. Boundaries of the substrata were not measured in these experiments; encounter probabilities of the two test substrata were assumed to be equal. Each experiment was replicated. The distribution of plantigrades was not significantly different from random attachment expectation in any of these experiments. About half (87/180) of the plantigrades used in these experiments were unattached or attached to the glass finger bowl. The conclusions from these experiments are similar to those obtained from the four-way choice experiments: none of the substrata tested appear to be strongly preferred by *M. californianus* plantigrades.

DISCUSSION

Some marine mussels, particularly *Mytilus edulis* studied in Europe, go through two attachment phases called primary settlement and secondary settlement (BAYNE, 1964, 1976; SEED, 1969). As larvae settle from the plankton, they test various substrata and select a primary attachment site (primary settlement). Primary settlement is often on a filamentous alga (BAYNE, 1964; PAINE, 1974; PE-

Table 5

Results of two-way choice experiments with *Mytilus californianus* plantigrades. E is the expected number of individuals attached to this substratum based on the assumption of equal encounter probabilities. O is the observed number of attached plantigrades.

Substratum	O	E	χ^2
<i>Mytilus edulis</i>	5	6.0	0.1 NS
<i>Rhodomela larix</i>	7	6.0	
<i>Mytilus edulis</i>	12	8.5	2.1 NS
<i>Rhodomela larix</i>	5	8.5	
<i>Mytilus californianus</i>	9	8.5	0.0 NS
<i>Rhodomela larix</i>	8	8.5	
<i>Mytilus californianus</i>	5	9.5	3.4 NS
<i>Rhodomela larix</i>	14	9.5	
<i>Mytilus californianus</i>	7	6.5	0.0 NS
<i>Mytilus edulis</i>	6	6.5	
<i>Mytilus californianus</i>	4	7.5	2.4 NS
<i>Mytilus edulis</i>	11	7.5	

NS = Not significant.

TERSEN, 1984). Secondary settlement is movement and reattachment of small mussels, usually when individuals are greater than 1.0 mm (BAYNE, 1964). Movement is often onto an established mussel bed (BAYNE, 1964). BAYNE (1964) suggested this behavior reduces competition between juvenile and adult *M. edulis*. Whether *M. edulis* has similar behavior on American shores is not known (SUCHANEK, 1978).

Studies on settlement and distribution of small *Mytilus californianus*, including this paper, have not demonstrated secondary settlement behavior in this species (PAINE, 1974; PETRAITIS, 1978; SUCHANEK, 1981; PETERSEN, 1983). In laboratory choice experiments, *M. californianus* larvae preferred adult clumps of *M. edulis* (PETERSEN, 1984). In field samples, *M. californianus* has been found on a variety of substrata, particularly filamentous algae and byssal threads of adult mussels (PAINE, 1974; SUCHANEK, 1979; PETERSEN, 1984). These results suggest that *M. californianus* settles broadly if its preferred substratum, *M. edulis*, is unavailable. In areas where *M. edulis* patches are common, *M. californianus* may select these patches over other available substrata; however, more work needs to be done on settlement preferences in the field.

Mytilus californianus settlers survive to the plantigrade stage on a variety of substrata. Only bare rock and barnacle-covered rock were barren of *M. californianus* plantigrades, although densities were fairly low in some patches of algae, such as *Polysiphonia* sp. Some surface cover is apparently necessary for larval settlement and plantigrade attachment.

Algal and mussel patches undoubtedly have many crevices and holes where plantigrades can attach and receive some protection from wave battering and predators. Plan-

tigrades are often found in the axils of thalli, in the crevice between adult mussel valves, and in cracks in rocks. Such microhabitats offer physical protection, and plantigrades may also be more secure when their byssal threads are attached to many different surfaces, rather than just one flat surface.

Differential predation rates might also explain the distribution of plantigrades. Many animals, including sea-stars, gastropods, crabs, and birds, are known to prey upon mussels (e.g., NORTON-GRIFFITHS, 1967; HARGER, 1972b; PAINE, 1974; SEED, 1976).

Some shore birds—e.g., Surf Birds, *Aphiza virgata* (Gmelin), and Black Turnstones, *Arenaria melanocephala* (Vigors)—prey upon small mussels along the central Oregon coast, eating both *Mytilus californianus* and *M. edulis* (Chris Marsh, personal communication). Searching by these birds may be more efficient on bare and barnacle-covered rock surfaces, leading to complete removal of all recent settlers and plantigrades. Predation in algal patches could be less efficient because some plantigrades might be overlooked by the birds and thus survive. *Nucella emarginata* (Deshayes, 1839) is an important gastropod predator on large mussels, particularly *M. edulis* (PARIS, 1960; DAYTON, 1971; HARGER, 1972b; SUCHANEK, 1978), but no studies have concentrated on the effects of this snail on plantigrades. Many small mussel shells with gastropod bore holes were found in the samples of algae and mussels collected at Mussel Reef. Plantigrades are undoubtedly eaten by these gastropods although the intensity of predation in different patches is unknown. *Nucella* enclosure experiments were attempted but were unsuccessful because of severe weather and vandalism. The role of other predators in controlling the abundance and distribution of small *M. californianus* has not been investigated although there has been speculation on this subject (SUCHANEK, 1979).

The primary settlement behavior (PETERSEN, 1984) and plantigrade survival patterns of *Mytilus californianus* may help to explain how mussel beds are established and persist through a broad geographic range. *Mytilus californianus* forms extensive beds on exposed rocky shores from Mexico to British Columbia (SOOT-RYEN, 1955; SUCHANEK, 1981). Disturbances occur periodically within this range, removing patches of established mussel beds (DAYTON, 1971; personal observation). Succession within cleared areas culminates in new *M. californianus* beds which persist until another disturbance occurs. In Washington, patches are filled by algae, *M. edulis*, and finally *M. californianus*, which settles among *M. edulis* patches and eventually excludes this competitively inferior mussel (PAINE, 1974; PAINE & LEVIN, 1981). However, because *M. edulis* is not very common on central Oregon shores (PETERSEN, 1983), and perhaps in other local areas, the recovery pattern may be somewhat different.

If *Mytilus edulis* patches were required for *M. californianus* colonization, the sequence leading to mussel bed recovery would be incomplete in geographic areas where

M. edulis is sparse. However, *M. californianus* larvae begin to settle once a disturbed area has been colonized by algae. Continual reproduction and broad larval preferences ensure that some settlement will occur on various algae. Pediveligers attach to many surfaces (PETERSEN, 1984) and plantigrades survive on most substrata, particularly those with small holes and crevices. This general attachment behavior of *M. californianus* pediveligers and their survival on diverse substrata assure a broad distribution of growing mussels in the disturbed area. As plantigrades grow, they gradually fill the original disturbed patch, attach to the rock, and exclude other species (PAINE & LEVIN, 1981). The dynamics of patch recovery may be altered because the survivorship rate of *M. californianus* is probably different in algal patches than in *M. edulis* patches, but the mechanism for mussel bed recovery remains intact.

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Observations on the Spawn of Three Species of *Conus* from the Golfo Triste, Venezuela

by

PABLO E. PENCHASZADEH

INTECMAR and Departamento de Estudios Ambientales, Universidad Simón Bolívar,
Apartado 80659, Caracas, Venezuela

Abstract. The spawn of three species of southern Caribbean Conidae was studied. *Conus spurius* differs strikingly from all other known species of the genus by having the largest recorded eggs (690 μm in diameter) and the fewest eggs per capsule (23-83); the hatching stage is a veliconch with a shell length of 1300 μm . The spawn of *C. centurio* is also noteworthy. The eggs of most *Conus* species are either large or small; however, those of *C. centurio* are intermediate in size (275 μm). The number of eggs per capsule is 1750 in this species, and the hatching stage is a free swimming veliger 320 μm in shell length. Egg capsules of the third species, *C. ermineus*, contain an average of 2373 embryos each, and the larval shell on hatching is 295 μm in length.

INTRODUCTION

THE FAMILY Conidae is represented by a large number of species distributed mainly in the tropical and subtropical seas. Characteristics of spawning have been studied for many species, especially those from the Pacific and Indo-Pacific oceans (RISBEC, 1932; THORSON, 1940; OSTERGAARD, 1950; NATARAJAN, 1957; KOHN, 1961a, b; PERRON, 1981a, b, c, 1983). In the Caribbean area, research has been done on several species (LEBOUR, 1945; D'ASARO, 1970; BANDEL, 1976). Data on more than 45 species suggest that there is a common pattern for the egg mass and a single type of egg capsule. However, specific differences are present in the arrangement of the egg capsules and their size and shape, and in the number and diameter of the eggs.

This study describes the egg masses, capsules, eggs, and hatching stage of three species of *Conus*: *C. spurius* Gmelin, 1791, *C. centurio* Born, 1778, and *C. ermineus* Born, 1778. Several of the features described are uncommon among conids.

MATERIALS AND METHODS

Five adult specimens of *Conus spurius* were obtained by trawling at 35-40 m depth in the Golfo Triste (January 1977). These were kept in a non-circulating seawater aquarium, 22-28°C, with a mixed substratum of sand and small stones. Two egg masses laid by a single individual on the walls of the aquarium were obtained. Four speci-

mens of *C. centurio* were obtained from a depth of 42 m (February 1977) and maintained in aquaria as above. These produced five egg masses on the walls of the aquaria, as well as one on the shell of one of the adults.

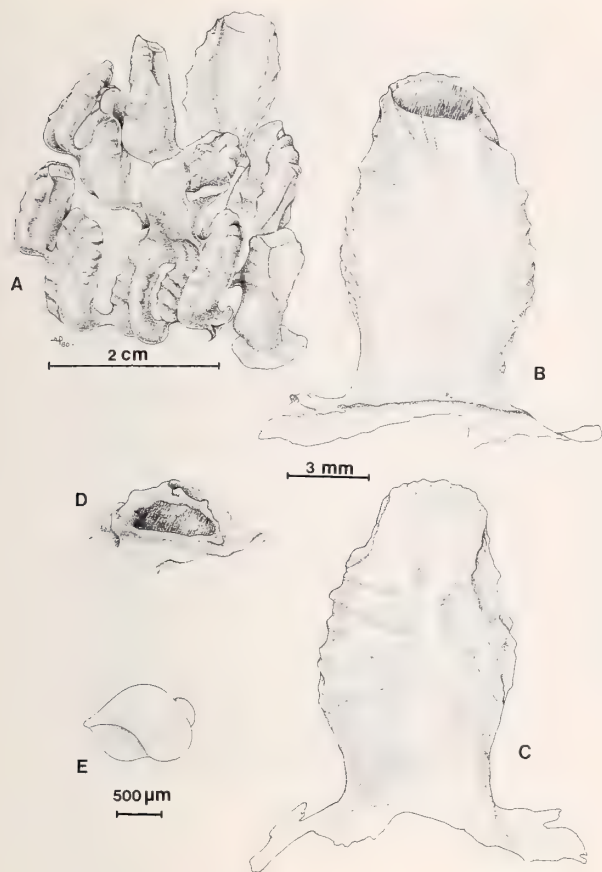
Egg masses collected from nature during trawls in the Golfo Triste at depths between 35 and 45 m were also studied (three of *C. spurius* and three of *C. ermineus*). A total of nine adult *C. ermineus* were maintained in aquaria but never laid egg masses.

RESULTS

Conus spurius

The two egg masses laid in the aquarium consisted of 18 and 21 egg capsules respectively. The capsules were arranged in levels; some were attached by a basal membrane to the substratum (the aquarium wall) and additional egg capsules were attached to the original ones. Other capsules were attached to the second layer, and so on to form six layers (Figure 1).

The egg capsule has a tongue-like shape, with a pre-formed, sub-oval exit aperture closed by a transparent membrane at the upper extreme. The strong walls of the egg capsule are opaque white, with noticeable wrinkles. The dimensions were 11.2-13.2 mm high, 7.3-9.1 mm wide, and 3.0-4.0 mm thick. Egg masses collected in nature had 32, 17, and 27 egg capsules identical to those described above.



Conus spurius. A. View of a fragment of an egg mass. B. Front view of an egg capsule. C. Back view of an egg capsule. D. View of the tip of an egg capsule. E. Outline of the shell at hatching.

Egg number in capsules was constant for each egg mass, but there was wide variation between the different egg masses examined. In the egg masses obtained in the laboratory, we counted between 23 and 36 eggs per capsule, whereas in the egg masses collected in nature, we found 23–36, 41–53, and 76–83 embryos in each egg capsule. The number of eggs seemed to be related to the size of the egg capsule.

Uncleaved ova measured between 687 and 707 μm in diameter (mean 690 μm). All of the embryos developed, and the shell size at hatching was 1200–1302 μm (mean 1297 μm), both in egg masses collected from the aquarium and from nature. The crawling stage was a veliconch with a well-developed foot and a very small velum.

Conus centurio

We obtained a total of 32 egg capsules on the aquarium walls, ordered in rows with as many as 8 egg capsules per row. An egg mass consisting of 13 capsules was also laid on the shell of one adult *C. centurio* (Figure 2).

The egg capsules were leaf-like and asymmetrical when seen from the front, with one side more developed than the other; they were almost completely transparent. The sizes of the egg capsules were very constant, being 12.8 mm high, 7.8 mm wide, and 3.1 mm thick. The capsules were not arranged in levels. In each capsule, 1731 to 1772 eggs developed. The uncleaved egg diameter was 275 μm , and the shell size of the free swimming veliger at hatching was 320 μm . Hatching occurred through a preformed, elongate escape aperture at the top of the egg capsule (Figure 3).

Conus ermineus

Three egg masses assigned to that species, common in the Golfo Triste, were found at depths between 30 and 50 m, and contained 13, 19, and 31 egg capsules respectively. The egg capsules were arranged in layers, the first of which was attached directly to the substratum (an empty shell in the three cases) with the other egg capsules attached to the first. Three layers were found in two egg masses, whereas the third egg mass consisted only of a row in a single layer. The flattened, white egg capsules were leaf-like, with relatively weak and semi-transparent walls, and bore large, superficial and transverse wrinkles. The mean size of egg capsules was 18.8 mm high, 15.3 mm wide, and 2.0 mm thick. In each egg capsule, between 2221 and 2420 embryos (mean 2373) developed, hatching as free swimming veliger larvae. The size of the larval shell upon hatching was 295 μm . Escape was made through a very elongate, preformed aperture at the top of the capsule on the upper margin (Figure 4).

DISCUSSION

There are major differences within the genus *Conus* in regard to the number of eggs per capsule and the egg diameter. A review of the literature indicates that an inverse relation exists between the two (Figure 5). Of the many species studied by KOHN (1961a, b), all of those characterized by small egg diameters hatched as free swimming veligers; he found no species with nurse eggs. In contrast, OSTERGAARD (1950) reported that in the large-egged *C. pennaceus* (egg diameter 460 μm ; 80 eggs per capsule) eclosion takes place at a veliconch stage, virtually without a pelagic stage (not more than one day in the plankton). PERRON (1981a, b, c, 1983) has confirmed Ostergaard's observations on *C. pennaceus* and has found between 25 and 250 ova per capsule. Another Pacific species, *C. glans*, also produces eggs with large diameters (440 μm) and hatches as a veliconch with little or no pelagic stage (KOHN, 1961b). *Conus araneosus* from India has large eggs of 467–517 μm (NATARAJAN, 1957), but details of hatching are unknown. Furthermore, our results on *C. spurius* indicate that this species has the largest egg diameter among those reported for the genus, as well as the lowest number of ova per capsule. The shell size on hatching is, with *C. pennaceus*, the largest registered (880

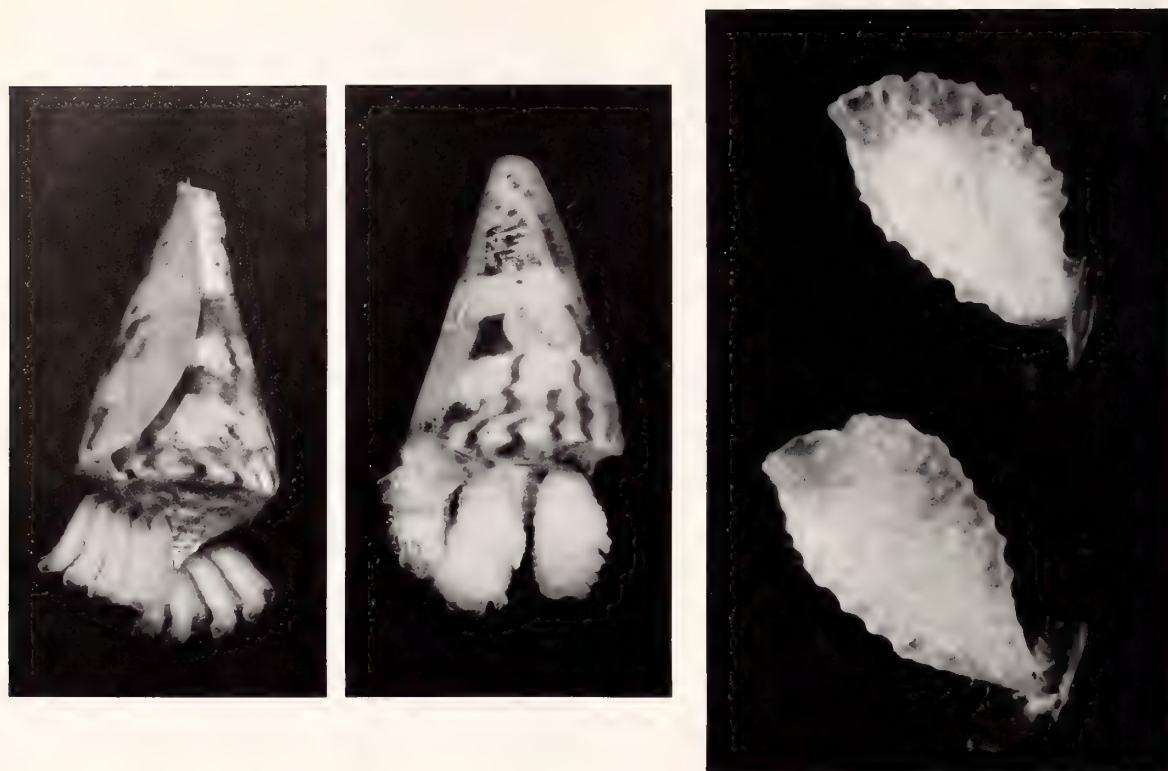
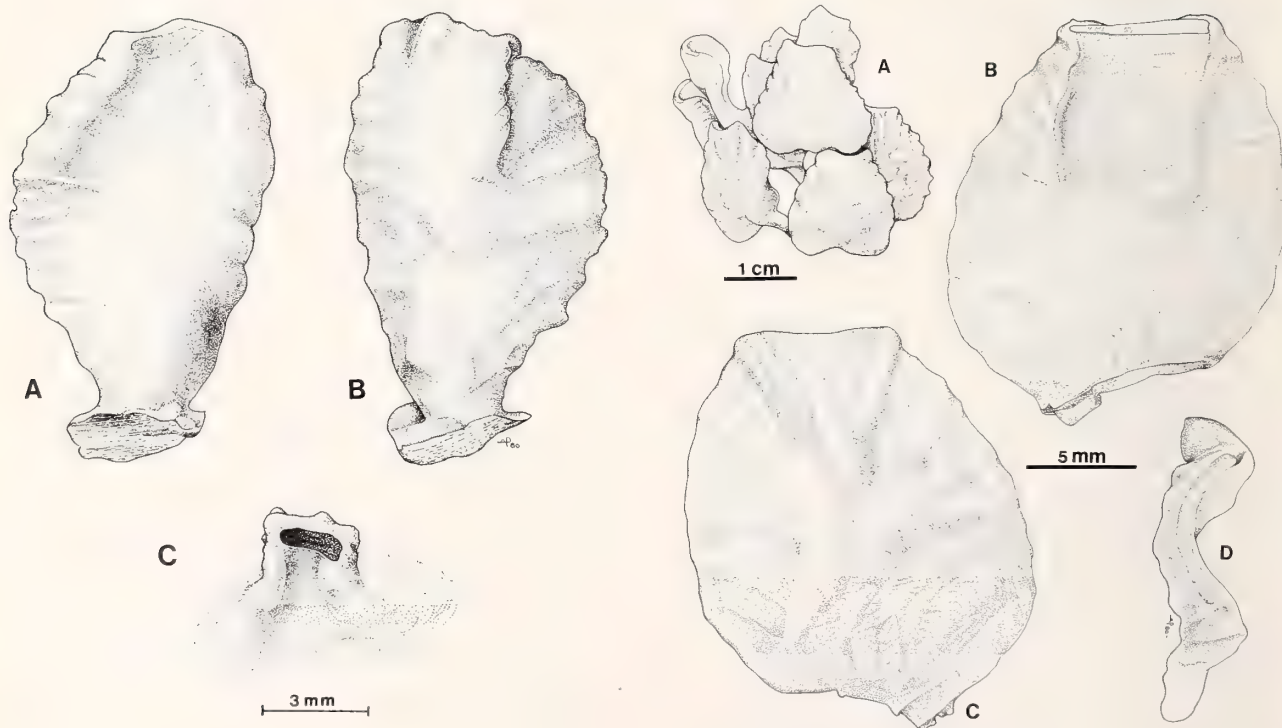


Figure 2

Conus centurio. Spawn attached to an adult *C. centurio* (natural size) and detail of two egg capsules ($3\times$).



Conus ermineus. A, B, and C. Front (A), back (B), and tip (C) views of an egg capsule.

Conus ermineus. A. View of a fragment of an egg mass. B, C, and D. Front (B), back (C), and tip (D) views of an egg capsule.

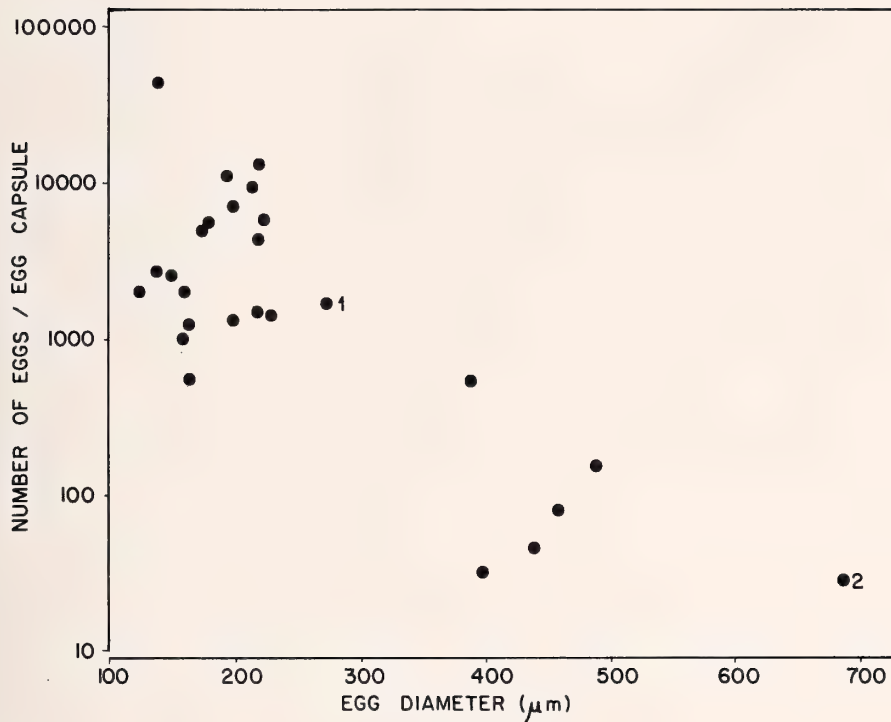


Figure 5

Number of eggs per egg capsule and egg diameter, for 26 species of *Conus*. 1 = *C. centurio*, 2 = *C. spurius*; other data taken from KNUDSEN (1950), OSTERGAARD (1950), NATARAJAN (1957) and KOHN (1961a, b).

μm in *C. glans*, KOHN, 1961b; 1100 μm in *C. araneosus*, NATARAJAN, 1957; 1200–1250 μm in *C. pennaceus*, OSTERGAARD, 1950, and PERRON, 1981a). The characteristics of the hatching form in *C. spurius* suggest no pelagic stage or a very short time in the plankton. However, D'ASARO (1970) studied the spawn of *C. spurius atlanticus* from Florida, and suggested that development in this subspecies indicated a planktotrophic veliger stage; he found 59 eggs per capsule, but did not report egg diameters, size, or characteristics of the hatching stage.

The eggs of most *Conus* species are either large or small (Figure 5). Those of *C. centurio*, however, are intermediate in size, and, together with those of *C. textile* and *C. striatus* (PERRON, 1981b), they provide the only recorded examples of *Conus* eggs with diameters between 240 and 340 μm .

The pattern exemplified by *C. ermineus* is more common: large numbers of eggs per egg capsule and small egg diameters, with hatching taking place as veliger larvae that presumably remain in the plankton for some time. It is interesting to note, however, that BANDEL (1976), studying Colombian material, reported *C. ermineus* egg capsules with a considerably lower number of eggs ("about 500") than found by us in the Golfo Triste (about 20% of our totals).

The egg mass of *C. spurius* has all the characteristics reported by D'ASARO (1970) for *C. spurius atlanticus*, and

it is also very similar to the description given for the Indo-Pacific *C. pennaceus* in the arrangement of the egg capsules in layers and in having decurved capsules (OSTERGAARD, 1950; KOHN, 1961b). In *C. ermineus*, egg capsules are arranged in rows in a single layer as BANDEL (1976) described, or in as many as three layers; egg capsules of *C. ermineus* were the largest egg capsules we recorded in the Golfo Triste *Conus* material.

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The Rhythmic Activity of *Nautilus pompilius*, with Notes on its Ecology and Behavior in Fiji

by

LEON P. ZANN

Institute of Marine Resources, The University of the South Pacific,
Suva, Fiji

Abstract. Specimens of *Nautilus pompilius* were trapped on the sea floor in depths of 450 to 500 m off Suva, Fiji. As found in other studies, these were mainly mature (mean shell diameter 13.3 cm, range 10.3–15.2 cm; $n = 74$) males (90–94%). Eleven individuals were kept under simulated natural conditions (0.1 lux daylight intensity; 10–15°C) and activities were recorded constantly for a total of 80 days. Activity was characterized by bursts or periods of swimming (minor during the day; 5–12 min at night) every 30 to 50 min. These were termed “subcycles.” Activity was crepuscular/nocturnal. Healthy, freshly collected specimens swam for an average of 160 min/day: 2.6 min/h during daylight, 11.9 min/h at dusk, 7.0 min/h during night, and 6.2 min/h at dawn ($n = 4$; 25 days of records). A rhythm comprising an innate subcycle of 30 to 50-min periodicity, modified by daily cycles of photoperiod, and an endogenous 24-h periodicity is proposed. Aquarium behavior is related to the natural habitat. It is proposed that the subcycles of activity are a strategy for hunting and scavenging in a homogenous environment where food is limited. *Nautilus* swam about 1600 m/day, of which most (1350 m) was at night. It is, therefore, unlikely that the population studied migrate at night to the nearest reefs (6000 m away) as suggested elsewhere. Brief notes are also included on the habitat, aquarium behavior, and growth rates of *Nautilus* in captivity.

INTRODUCTION

THE FOUR species of living *Nautilus* (SAUNDERS, 1981) are relicts of a large group of shelled cephalopod mollusks that flourished in the world's seas from the Triassic to the Tertiary, 225 to 65 million years ago. Because of the importance of the nautiloids and ammonoids in the fossil record, paleoecologists have shown considerable interest in establishing the ecology, behavior, and life history of living *Nautilus*, which are little known because of their deep water habitat and restricted distribution.

The present study investigates the activity patterns of *Nautilus pompilius* Linnaeus, a species found in depths of 100 to 650 m on reef slopes in the Philippines, Indonesia, New Guinea, Solomon Islands, possibly northeastern Australia, Vanuatu, and Fiji (WARD *et al.*, 1977; SAUNDERS, 1981).

A number of studies indicate that the *Nautilus* species are nocturnal. WILLEY (1902) suggested that they move up reef slopes from deepwater at night. BIDDER (1962) noted that captive *N. macromphalus* swam chiefly at night and spent most of the day at rest on the bottom. HAVEN

(1972) described Philippine *Nautilus pompilius* as “diurnal” in activity, as only baited traps left overnight caught specimens. WARD *et al.* (1980) reported that the New Caledonian *N. macromphalus* had been observed swimming actively near the surface at night by divers, indicating that they are inactive during the day or migrate into deep waters. Carlson (DUGDALE, 1982 and personal communication) has evidence from specimens of *N. belauensis* released with telemeters that suggests that this species does move vertically, from 400 m to 100 m, at night.

Although specimens of *Nautilus* have been successfully kept in aquaria for periods of up to one year (JECOLN, 1980), there have been only superficial observations on their activity cycles. *Nautilus macromphalus* kept in aquaria in New Caledonia and Japan were reported to be active after sunset (MIKAMI & OKUTANI, 1977; JECOLN, 1980), and HAVEN (1972) noted that *N. pompilius* in aquaria in Philippines became active at dusk. HAYASAKA *et al.* (1982) made two days of visual observations on captive *N. pompilius*, and found they were most active at about dawn on both mornings. They concluded: “As far as our observa-

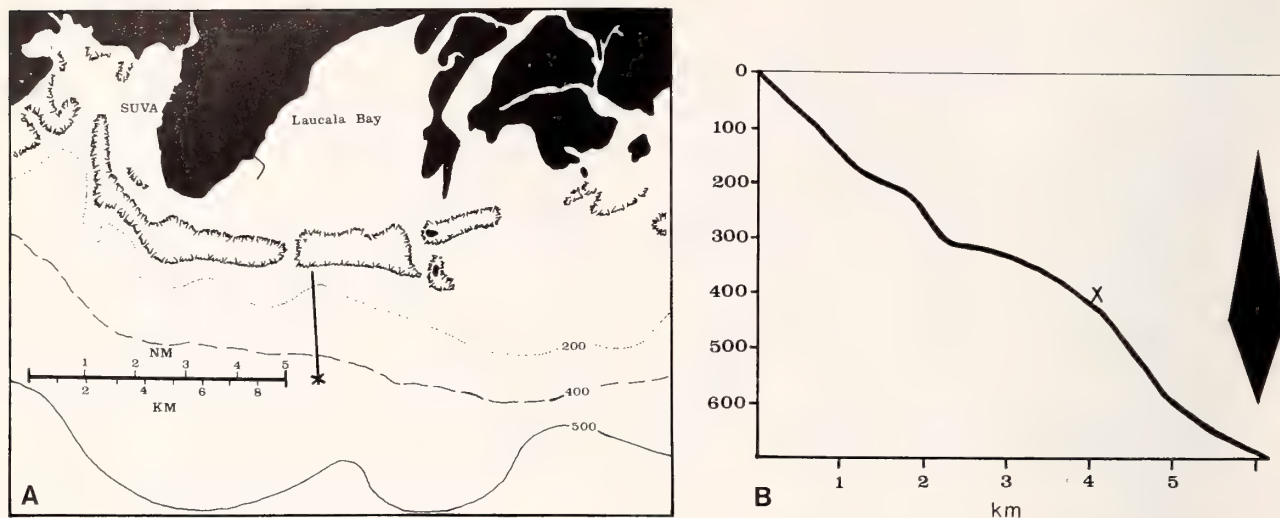


Figure 1

A. Collection site (x) off Suva Reef, Viti Levu Island, Fiji. B. Depth profile (meters) along transect in A, with kite diagram (arbitrary scale) of *Nautilus* distribution.

tions are concerned, it is hard to say that *Nautilus* is a nocturnal animal." A histogram of the data presented in HAYASAKA *et al.* (1983) also shows some activity after sunset ("lights-off") and a major peak before dawn ("lights-on"); the authors considered that this activity may have been induced by the bright lights of the display aquarium.

In the present study, the swimming activity of 11 specimens of *Nautilus pompilius* held under simulated natural conditions of temperature and light was continuously monitored by activity recorder. Light and temperature regimes were also manipulated in an attempt to establish the nature of the rhythmicity. As little is known of the ecology or general behavior of *Nautilus*, some associated observations are also presented as a background to the study of swimming rhythmicity.

MATERIALS AND METHODS

Specimens of *Nautilus pompilius* were captured in chevron-shaped fish traps (1.80 × 0.9 × 0.6 m; conical entrance 20 cm in diameter) set on the sea floor at depths of 400 m to 500 m off Suva, Fiji (Figure 1). To determine whether *Nautilus* were leaving the bottom, four smaller traps were also placed at 20-m intervals from the bottom on the mooring line. The study site, 8 km south of the University of the South Pacific, was 4–5 km south of Nukubuco reef, and about 7 km east of the area where WARD *et al.* (1977) collected their *Nautilus*. Slightly decaying skipjack tuna was the most effective bait used. Initial surveys indicated that *Nautilus* was most abundant at 450–500 m. A total of 150 underwater photographs was taken of this area with a bottom-triggered Ewing deep-water camera.

Ninety specimens of *Nautilus* were obtained from eight trap series that were set at two to six week intervals between September 1982 and April 1983. Average catch per trap per day was 3.1 individuals (range 1.0–8.3). On each occasion two or three specimens were quickly returned to the laboratory in darkened containers of cooled seawater while other captives were either preserved or measured, tagged, and released. No recaptures were made.

Each *Nautilus* was held in a dark-sided, 100-L capacity aquarium of recirculating, charcoal-filtered and refrigerated seawater (10–14°C; salinity 34.5–35.5‰). The aquaria were kept in a darkroom that could be indirectly illuminated by a 15-cm diameter skylight with a 10 × neutral-density filter to further reduce light intensity. This illumination, of about 0.1 lux at mid-day and very dim to human eyes, approached that of natural conditions (0.004% of surface intensity of 470 nm light at 500 m). Artificial light, when necessary, was provided by indirect illumination from a 40-watt fluorescent light (approximately 2 lux). A red photographic safelight provided illumination when servicing the equipment in darkness. Disturbances were restricted to a daily instrumentation check and weekly feeding, cleaning, and water change. When available, several live deepwater carid shrimps, a possible prey of *Nautilus*, were left in the aquarium to provide a regular food source. At other times, *Nautilus* were fed on shrimp and fish during the day, although this tended to increase the duration of daytime activity.

Nautilus lived for up to three months under these conditions; they fed regularly and grew various amounts. However, all specimens became positively buoyant—they are usually neutrally buoyant—after several days of captivity.

Swimming activity was monitored directly and indi-

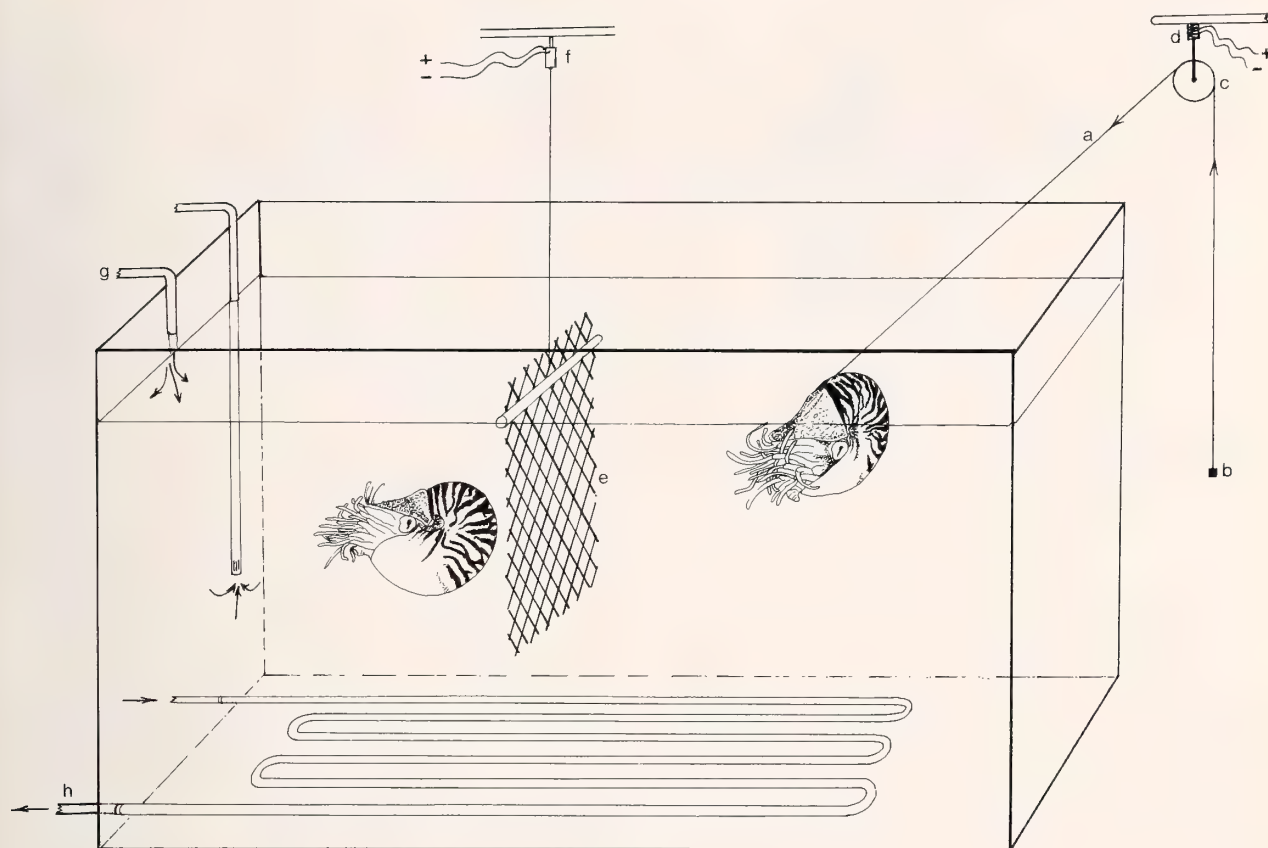


Figure 2

Activity recorders. Movements in a thread (a), counterweighted (b) and redirected by a pulley (c), were detected by a strain-gauge (d), amplified and recorded. Alternatively, a plastic wire panel (e) was suspended from a strain-gauge (f) that recorded a signal if touched by a swimming *Nautilus*. A single animal was placed in each dark-sided tank; water was constantly filtered (g) and cooled (h).

rectly. In the direct method, a cotton thread was glued with quick drying "Superglue"TM to the dorsal surface of the shell, and passed through a small pulley fixed above the aquarium to a light counterweight (1 to 2 g) which kept tension on the thread. An engineering strain gauge, fitted to the pulley, detected any slight movement in the system. A slow-speed (10 cm/h) chart recorder recorded an amplified signal. The behavior of the *Nautilus* did not appear to be influenced by the slight friction of the pulley and counterweight but, to test this, an indirect recorder was also used for several experiments. This consisted of a rectangular plastic wire panel, weighted at the bottom and equipped with a float at the top, directly attached by thread to the strain gauge. To swim from one end of the tank to the other, the *Nautilus* had to make contact with the panel. Small, local movements were not detected. Because of the possibility of changes in behavior resulting from acclimation to the artificial conditions and activity recorder, *Nautilus* were usually replaced by freshly collected specimens after one week.

RESULTS

General Ecology and Aquarium Behavior

The outer-reef slope of Suva barrier reef initially slopes steeply to about 200 m depth, then more gradually to 500 m at about 4–5 km from the reef (Figure 1A). *Nautilus* were trapped in shrimp traps between 100 and 600 m, and were most abundant at 450–500 m (King, personal communication). No *Nautilus* were ever trapped in the traps suspended above the bottom, indicating that they rarely if ever leave the sea floor. Underwater photographs of the sea floor showed a uniformly soft bottom of terrigenous clays from the nearby Rewa River, highly bioturbated by polychaete and other burrowers. No *Nautilus* were seen in 150 frames, covering about 3000 m² of sea floor. Crustaceans trapped in this area included carid shrimps (*Heterocarpus*; *Plesionika*; *Parapandalus*), galatheids (*Munida*), majid crabs (*Myra*; *Hyastenus*), goneplacids (*Geryon*), portunids (*Carybdis*), homolids (*Homola*), several pagurids (*Parapagurus*, etc.), and panulurids. Several

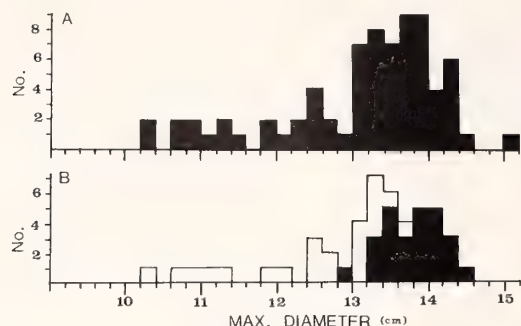


Figure 3

A. Size frequency distribution of *Nautilus* captured. These were collected from the same site over a 6-month period. B. Subsample of A, showing size of mature (black) and immature (white) specimens.

species of gorgonians, solitary corals, antipatharians, and hydrozoans, as well as a number of bivalves, gastropods, holothurians, ophiuroids, and echinoids were dredged from this area. A large number of species of fishes have been collected from the 100–600 m zone of Fijian reef slopes (Raj & Seeto, unpublished data).

Epizoites were present on some *Nautilus* shells. Clusters of between two and six of the small pedunculate barnacle *Temnaspis excavatum* (Hoek) were present on the umbos and ventral part of the shell, near the hyponome, of about 15% of *Nautilus* specimens. This barnacle has previously been recorded attached to isopods, crabs, and other barnacles from 200 to 400 m depths in the Indo-Pacific (Foster, personal communication). Isolated serpulid worm tubes were present on about 5% of specimens. On average, five of the ectoparasitic caligid copepod *Anchicaligus nautili* (Willey) were present on the shell and soft parts of each of ten *Nautilus* carefully examined.

The mean shell diameter of the *Nautilus* collected was 13.3 cm (mode 13.8 cm; range 10.3–15.2 cm; $n = 74$; Figure 3A). In the other studies of *Nautilus* off Suva, WARD *et al.* (1977) reported a mean diameter of 14.16 cm ($n = 22$) and TANABE *et al.* (1983) of 13.5 cm ($n = 31$). The shells of Fijian *N. pompilius* are variable in coloration. In about 60% of the shells, bands extended to the umbo and in the remainder they did not (termed variants A and B respectively by WARD *et al.*, 1977). Of 50 specimens dissected, three were females and two immature specimens were probably females—i.e., only 6% to 10% were females. WARD *et al.* (1977) reported 14% females, and TANABE *et al.* (1983) reported 25% females in their Fijian studies. About half the sample examined (26 of 49) had definite eye notches, indicating their maturity. Notches appeared at 13.2–13.4 cm shell diameter, and all specimens above 13.8 cm had notches (Figure 3B). All studies of *Nautilus* since WILLEY's (1902) have found a similar anomalous predominance of males and an absence of juveniles, implying that the young and females either live

in other habitats or are not prone to trapping. Little is known of the life-cycle of *Nautilus*.

Freshly captured *Nautilus* were gorged on fish bait (average gut contents 51 g; range 4–85 g; $n = 10$), and fed little for the first week. They subsequently consumed about 20–40 g of dead shrimp per week, showing a preference for the head.

Immature specimens kept for two months in the aquarium showed some growth. Individuals 11.6 cm, 12.1 cm and 13.1 cm in shell diameter added 3.6 mm, 2.7 mm and 2.2 mm respectively to the apertural margin per month. Note that this represents an increase of spiral circumference of about 1%, and there was little measurable increase in overall shell diameter.

Three of 45 living specimens examined had triangular bites out of the apertural margin matching the gape of a *Nautilus* jaw. HAVEN (1972) proposed that these are received in intraspecific fighting. One juvenile drift shell from Suva (5.5 cm in diameter) had a fresh bite from the margin, suggesting that these fights might sometimes be fatal or, alternatively, that smaller *Nautilus* may sometimes be eaten by larger *Nautilus* or squid.

The swimming behavior and tentacle positions were similar to those described by HAVEN (1972). When resting, *Nautilus* attached to a solid object with one or two tentacles, and slowly rocked to-and-fro with its respiratory pulses. This was regularly interrupted by a few seconds of minor activity and repositioning. When feeding, *Nautilus* extended its tentacles and swam forward in BIDDER's (1962) "cone of search," but at other times *Nautilus* swam backwards. During periods of slow swimming, usually of about 3 to 10 min in duration, the tentacles were either trailing or in HAVEN's (1972) "cat's whiskers" pose, and any obstacles in the aquarium were carefully avoided. *Nautilus* generally took several hours to learn the spatial arrangements of the tank, and became quite adept at avoiding the activity panel. When alarmed, and occasionally spontaneously, for no apparent reason, *Nautilus* swam very vigorously for 30 sec to 2 min, often colliding with the sides of the aquarium. Tentacles were usually shortened during flight.

Of 11 *Nautilus* examined, 6 individuals (Specimens No. 1, 2, 5, 6, 9, and 10) remained active and fed regularly during the duration of the experiments, from 4 to 36 days. Specimen No. 4 died on the sixth day of recording; No. 7 and 11 were moribund during the first two days of recording and were terminated, and No. 8 was highly stressed for the first two days of recording and moved continuously. It was noted that most specimens that became moribund had enlarged spadices. An autopsy on one specimen showed that a newly formed septum had fractured, and a sliver of shell had perforated the viscera.

Activity Rhythms

About 80 days of activity records from 11 mature male *Nautilus* were obtained; of these, about 20 days were dis-

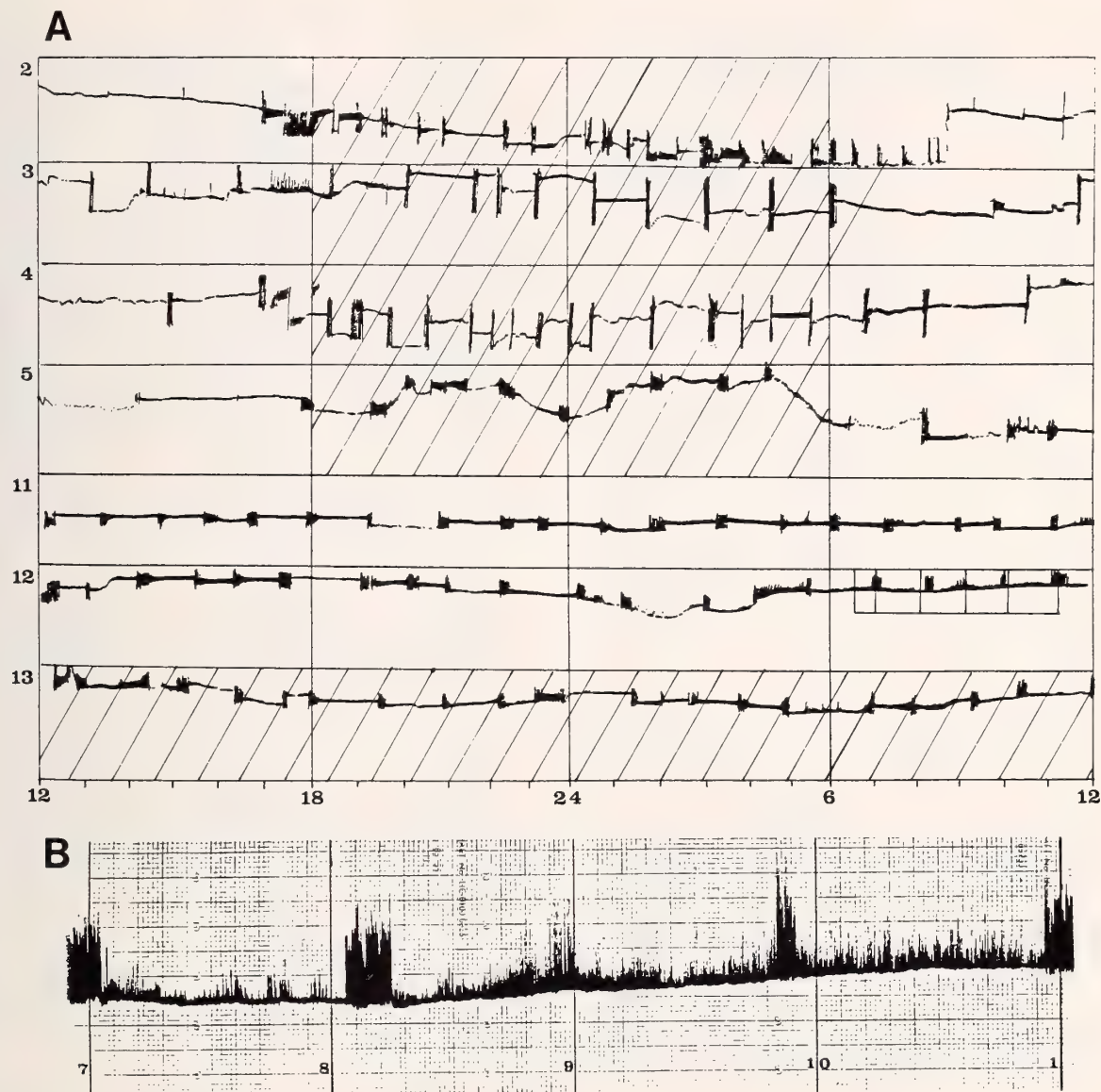


Figure 4

A. Actual records of activity of Specimen No. 1. Days 2 to 5 under normal photoperiod (L/D). Days 11 to 12 under constant light (L/L). Day 13 under constant darkness (D/D). Note subcycles of activity, especially under constant conditions. Differences in amplitude result from different gain settings on amplifier. B. Detail of recording for day 12. Horizontal axes: time in hours.

carded because of equipment malfunctions and erratic or moribund specimens. Malfunctions and power losses resulted in gaps of several hours in many records.

Records (Figure 4) clearly indicate the minor movements involved in position changing and the major movements of swimming activity above a thick baseline of electrical interference and shell rocking movements associated with the respiratory pulses. Activity was characterized by regular short periods or bursts of swimming of several minutes duration, followed by a longer period of inactiv-

ity. These are referred to as "subcycles" of activity. To determine whether the pattern of subcycles was a fatigue response due to the tethering to the activity recorder or to an innate pattern of activity, three *Nautilus* were tested in the panel activity recorder. These showed identical subcycles of activity and resting, indicating an innate behavior.

For analyses, the continuous records were arranged into hourly lots, and the duration of the swimming activity summed for each hour. The hourly activities of two *Nau-*

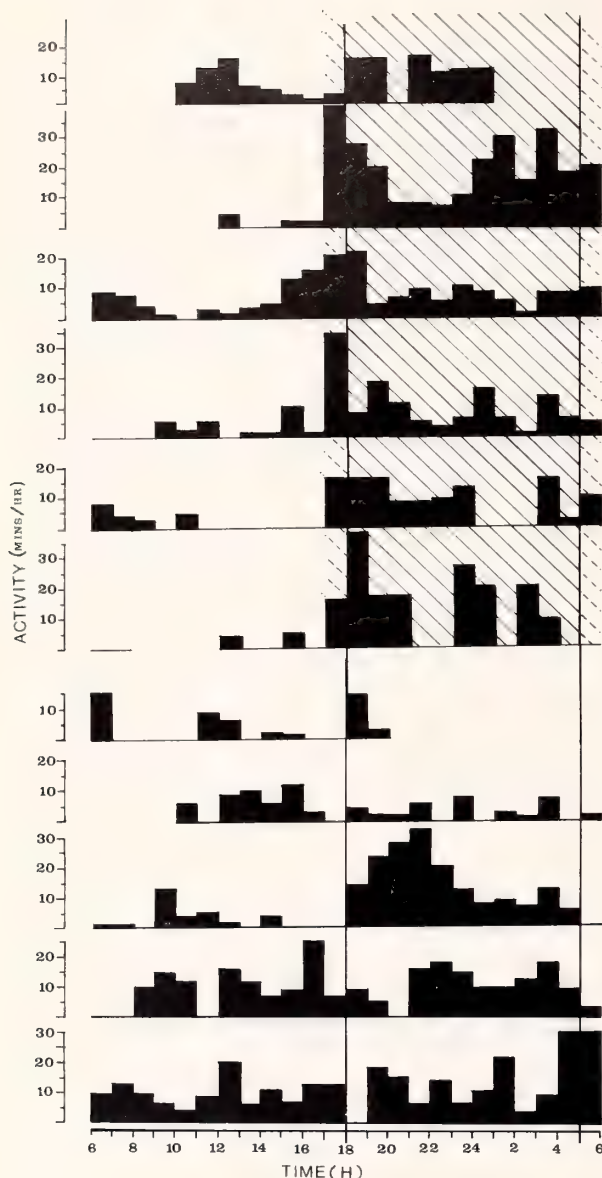


Figure 5

Summed activities for each whole hour, Specimen No. 1. Days 1 to 6 under normal photoperiod (L/D), days 7 to 11 under constant light (L/L). Shading represents night; dashed lines, dawn and dusk. Note nocturnal rhythm on days 2 to 6 (L/D) and on day 9 (L/L).

tilus over a total of 27 days are shown in Figures 5 and 6. Because the period of activity/inactivity was sometimes about one hour, hourly records may show alternate high and low activities, obscuring the general trend. Average activity for each hour of the day was therefore calculated to randomize sporadic activity or "noise," the subcycles, and the breaks in records. These show a pronounced nocturnal activity under "normal" photoperiod (Figure 7).

The activities of nine *Nautilus* over a total of 44 days

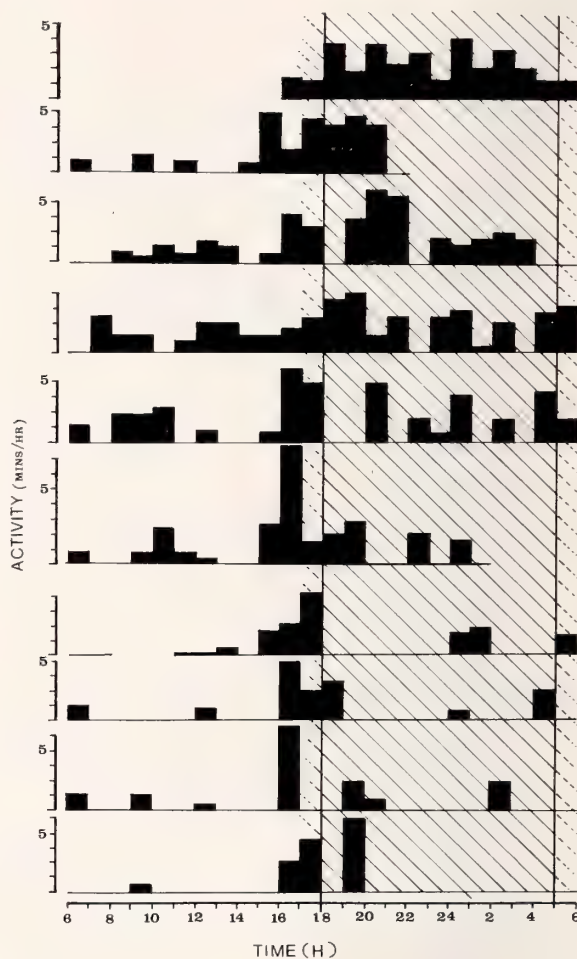


Figure 6

Summed activities for each whole hour, Specimen No. 9 (from partition recorder). The decline in activity after day 5 is partially due to an avoidance of the panel.

are analyzed in Table 1. The average duration of swimming per day varied from individual to individual, with the moribund specimen (No. 4) and the two tested under the less sensitive panel activity recorder (No. 9 and 10) least active. *Nautilus* swimming activity averaged between 52 and 188 min/day, with the higher figures (170–188 min/day) the more credible because of those specimens' good health in the aquarium.

The duration of swimming activity quickly declined in the moribund specimen and gradually declined in the healthy specimens (Figure 6). The duration of activity on successive days of recording of *Nautilus* Specimens No. 1, 2, 5 and 6 are illustrated in Figure 8. After initially high activities on the first day of capture (due to the stress of capture and exploration of the new surroundings) activity declined to between 120 and 160 min per day. Activity increased in No. 6 on days 7 to 9, and in No. 1 on day 6, the days of, and following, feeding.

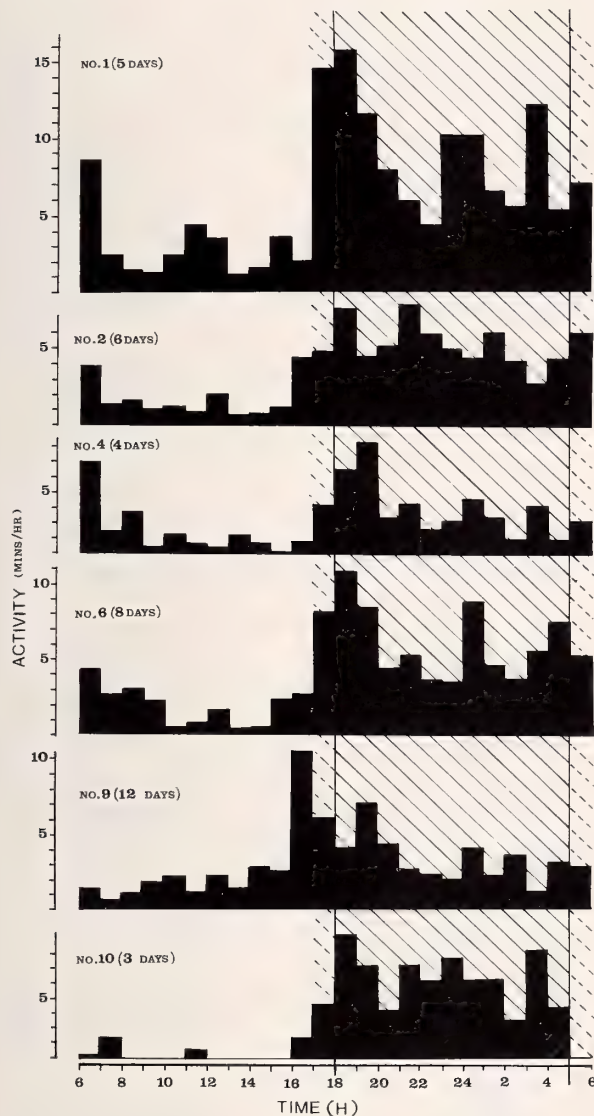


Figure 7

Average hourly activities of a number of days of recording (indicated) of six specimens. Note increased activity at dusk and anticipation of dusk in Specimens No. 2 and 9.

Under normal photoperiod, activity was lowest during the daylight hours (0700 to 1600) for all specimens on all days (average activities ranged from 0.9 to 3.0 min/h) (Figures 5 to 7; Table 1). Activity was highest at dusk (1600 to 1900) in all specimens (averages from 5.3 to 19.0 min/h) but continued throughout the night (averages from 2.3 to 9.3 min/h). Activity was not uniform during the night and several specimens showed three or four peaks of activity (including dusk) at about 4-h intervals. Dawn activity (0400 to 0700) was approximately similar to the nocturnal levels (averages from 1.1 to 8.7 min/h). Dusk activity often commenced before the actual dusk (e.g.,

Specimen No. 9, Figure 6). On several occasions *Nautilus* were held under artificial light during the day, and dusk occurred as a sudden "lights-off." In most cases, activity preceded "lights-off" indicating that *Nautilus* anticipate dusk and are not stimulated to move solely by fading afternoon light.

To further test whether the nocturnal activity was an exogenous rhythm (controlled solely by environmental cycles) or an endogenous one (controlled by an internal or innate "biological clock"), Specimen No. 1 was placed under constant conditions after a period of normal photoperiod (Figure 5). Unfortunately, the record for the first night was lost due to equipment malfunction; day 2 of constant light showed random activity; day 3 showed a clear nocturnal rhythm; and days 4 and 5 showed random activity. This animal was later subjected to five days of constant darkness; hourly records showed uniform or random activity with the regular subcycles of activity predominating.

To determine the effects of temperature on the duration of swimming activity and on the general behavior of *Nautilus*, three specimens were subjected to a range of temperatures between 11 and 19°C (Figure 9). The average activities for each day (expressed as min/h) for two specimens were variable, while the other was more uniform. No specimens showed any increase in activity at the higher temperatures although this had been expected on metabolic grounds.

The subcycles of activity were relatively regular in their period from activity to activity, and in the duration of the activity, but they differed somewhat from individual to individual. The average duration of swimming in each subcycle of activity for the first three days of recording for *Nautilus* Specimens No. 1, 2, 5, and 6 was 6.7 min (individual averages ranged from 4.5 to 11.9 min; $n = 300$ measurements). The period of the subcycles, the time from the commencement of one activity to the commencement of the successive activity, averaged 41 min (individual averages ranged from 31 to 51 min; $n = 300$) (Table 1).

DISCUSSION

Nautilus held under simulated natural conditions were mainly nocturnal with a pronounced peak of activity at dusk. Their behavior was characterized by brief periods of swimming, followed by periods of inactivity or resting, at about 30 to 50 min intervals. These were termed "subcycles" to distinguish them from the 24-h rhythmicity. During the daylight hours the activity was minor, ranging from brief repositioning movements to a minute or so of slow swimming. During the night *Nautilus* alternately swam for between 5 and 12 min at a time and rested for about 20 to 40 min.

Under normal photoperiod (L/D) all the *Nautilus* examined were more active at night. Four freshly collected, healthy specimens tested over a total of 25 days were ac-

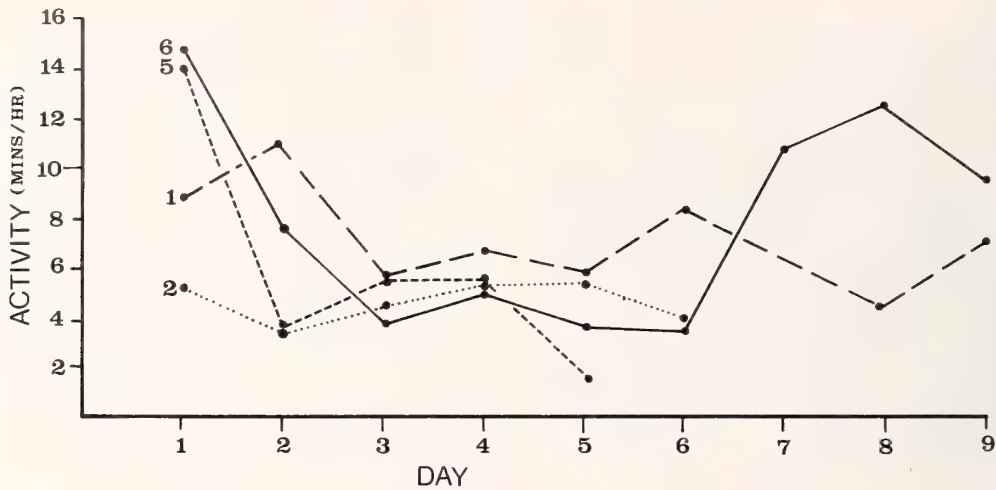


Figure 8

Daily activities (expressed as average activity in minutes per hour) of successive days of captivity for *Nautilus* Specimens No. 1, 2, 5, and 6.

tive for an average of 160 min/day. This period was not overtly affected by temperature (11–19°C range) although this might be expected on metabolic grounds. Their average activity during the hours of daylight was 2.6 min/h, at dusk 11.9 min/h, during the night 7.0 min/h, and at dawn 6.2 min/h.

The nocturnal rhythm did not persist under constant conditions of darkness (D/D) or light (L/L), but did reappear on one occasion after several days. However, because *Nautilus* regularly began moving an hour before dusk, before any decline in light intensity, the 24-h periodicity may be innate or endogenous.

The characteristic 5–12 min of activity each 30–50 min seen at night under normal photoperiod (L/D) continued for the entire 24 h under constant conditions of light (L/

L) or darkness (D/D). This suggests that the subcycles of activity are a basic or innate behavior, modified by environmental factors (light and darkness) and a 24-h endogenous periodicity.

Several workers have previously alluded to the short-term periodicity, but did not comment on its significance.

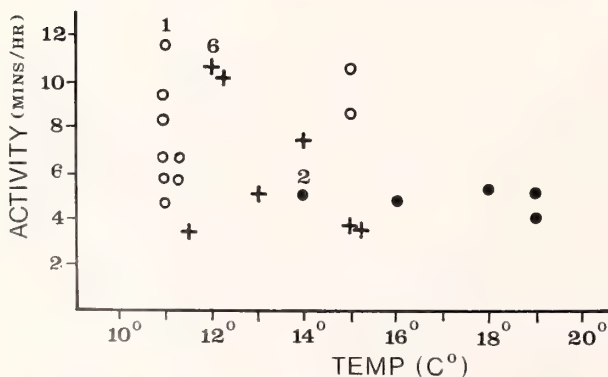


Figure 9

Daily activities (expressed as average activity in minutes per hour) of *Nautilus* Specimens No. 1, 2, and 6 at a range of temperatures.

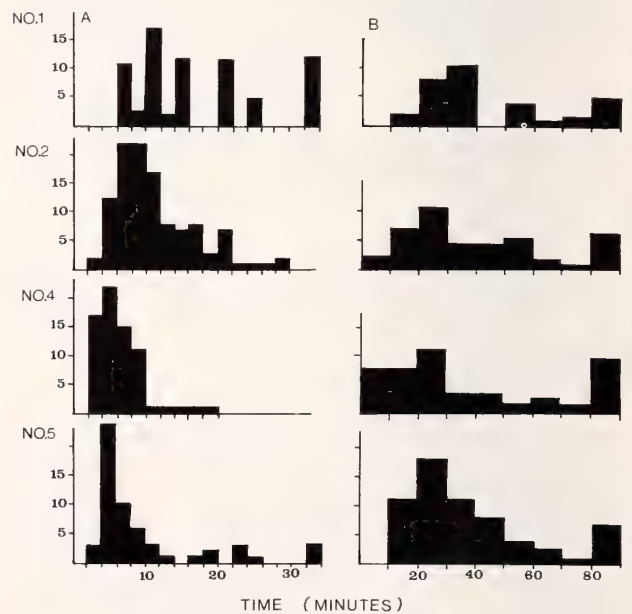


Figure 10

Frequency distributions of (A) duration of subcycle activity; (B) period from commencement of one activity to the commencement of the next, for the first three days of captivity of *Nautilus* Specimens No. 1, 2, 4, and 5.

Table 1
Analyses of activities of *Nautilus pompilius*.

	Nautilus specimen number										
	1	2	4	5	6	7	9*	10*	11*		
Days recorded	1-6	1-6	1-4	1-6	1-9	1-2	1-8	1-3	1-2	1-2	
Average temperature (°C) (range)	12 (10-14)	16 (14-19)	19.5 (19-20)	15 (10-22)	12 (10-14)	21 (21-22)	13 (12-14)	14 (13-15)	18	18	
Average activity per day (min) (range)	172 (106-261)	111 (84-125)	52 (38-72)	172 (30-312)	188 (80-360)	188 (65-312)	96 (80-132)	67 (27-87)	170	170	
Average activity (min) per hour of:											
Daylight	2.8	1.6	0.9	3.0	3.0	1.4	2.3	0.3	9.3	9.3	
Night	9.3	6.7	2.3	3.7	8.5	7.7	4.0	5.0	14	14	
Dusk	19.0	7.5	5.3	5.6	15.3	12.2	7.6	5.8	12	12	
Dawn	6.1	4.4	3.2	5.5	8.7	8.3	1.7	1.1	17	17	
Subcycles of nocturnal activity (min):							not analyzed				
Average duration of activity	11.9	5.7	2.5	4.9	4.5						
Average period from onset of activity to next activity	51	51	41	32	31						
Health in aquarium	good	good	poor: died	good	good	poor: mori- bund	good	good	poor: mori- bund	poor: mori- bund	
No. of days kept successfully in activity recorder	35 days	6 days	6 days	6 days	9 days	removed after 2 days	15 days	7 days	removed	removed	

* Recorded in panel activity recorder; others by direct attachment.

BIDDER (1962) stated that "from time to time an animal becomes restless and swims about until a new resting place is found" (presumably in the daytime), and HAYASAKA *et al.* (1983) observed that, over two days of visual observations, *Nautilus* "moved from 15–20 minutes and rested for 15–30 minutes repeatedly."

The alternating swimming/resting behavior may be a strategy for hunting and scavenging in the homogenous environment of reef slopes where food is scarce and intraspecific contacts infrequent. *Nautilus* is probably an opportunistic scavenger, evident from the gorged guts of the trapped specimens, and a carnivore, indicated by the regular feeding on live shrimps in the aquarium. Although underwater photographs showed a featureless soft bottom, no *Nautilus*, and few potential prey organisms, bait rapidly attracts a wide variety of species (KING, 1983).

A pronounced nocturnal rhythm in an animal living at a depth characterized by very low daylight intensity is anomalous, particularly because the "pin-hole camera" eye of *Nautilus* is far less sensitive to light, and of a far lesser visual acuity, than any lensed eye (HURLEY *et al.*, 1978). *Nautilus* may hunt using its olfactory sense at night, but its vision must be of some use during the daytime, a time when it is largely inactive. Alternatively, the eyes may be used for hunting caridean shrimps, one of the dominant animals of the reef slopes; these species are mainly nocturnal and release bioluminescent clouds when disturbed (KING, 1983).

From the aquarium studies of the duration of swimming and published estimates of velocity (average 0.17 m/sec; range 0.10–0.25 m/sec; WARD *et al.*, 1977), *Nautilus* would swim about 1600 m per day (260 m in daylight, 370 m at dusk, 670 m at night, and 200 m at dawn). This approximates some of the distances travelled by Carlson's telemetered *N. belauensis* (DUGDALE, 1982) which migrated into shallower waters at night. However, because of the distance to the nearest reef (6000 m) in this study, it is improbable that Fijian *N. pompilius* migrate in the same way.

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Form and Function of the Radulae of Pleurotomariid Gastropods

by

CAROLE S. HICKMAN

Department of Paleontology, University of California, Berkeley, California 94720

Abstract. Detailed examination of the radulae of *Pleurotomaria* (*Perotrochus*) *midas* Bayer, 1965, and *P. (P.) quoyana* Fischer & Bernardi, 1856, leads to new conclusions regarding the form and function of the radula of the most primitive extant marine gastropods. A number of morphological features are interpreted as mechanical adaptations for dealing with stress and efficient accommodation of teeth when the radula is not in use. The terminal structures of the characteristic pleurotomariid "bristle tooth" are found to lack the flexural stiffness that has been attributed to them. They are highly flexible and may lie in tangled disarray after use in feeding. Independent evolution of similar teeth in *Seila* A. Adams, 1861, an unrelated mesogastropod that also feeds upon sponges, suggests that the morphology is not ancient or phylogenetically constrained so much as it is functionally constrained. Independent lines of evidence suggest that the radulae of living pleurotomariids offer few clues as to the radular morphology of ancient marine gastropods and the primitive state of the molluscan radula.

INTRODUCTION

IT IS A matter of longstanding record that the living species of pleurotomariid gastropods share a peculiar radular morphology. Descriptions and line drawings (DALL, 1889; BOUVIER & FISCHER, 1899; WOODWARD, 1901; BARNARD, 1963; AZUMA, 1964; FRETTER, 1964, 1966; HYMAN, 1967; BOUCHET & METIVIER, 1982) have emphasized the numbers of different kinds of teeth and, especially, the presence of numerous plates terminating in "brushes," "tufts," or "bristles." The details of form and the inferred function of these teeth have not been considered closely, and the terms "brush" and "bristle" may be inappropriate and misleading in terms of functional and mechanical properties.

Use of the term "hystricoglossate" (HYMAN, 1976:236) to describe the pleurotomariid radula emphasizes the distinctness from more typical rhipidoglossate archaeogastropod radulae and reinforces the notion that the terminal structures of the unique teeth are mechanically stiff or of very limited flexibility. Data from gut contents and observations of the substrata from which specimens have been taken or observed alive suggest that the animals feed primarily by "grazing" on communities of encrusting invertebrates, predominantly sponges (WOODWARD, 1901; THIELE, 1935; YONGE, 1973; ROPER, personal communication, 1975; HICKMAN, 1976; ARAKAWA *et al.*, 1978). The bristle teeth have, therefore, been implicated as adaptations for sponge feeding, and WOODWARD (1901) pro-

posed that the bristles might be used to remove "flesh" from sponge spicules.

Examination of the radulae of two species over a range of magnifications with conventional light microscopy and scanning electron microscopy reveals a number of new features and permits reevaluation of the pleurotomariid radula. The primary objectives of this paper are to describe and illustrate the dentition, to reconsider the function of the "bristle teeth," and to consider the evolution of this peculiar morphology in relationship to a close convergence with structures in the radula of a sponge-feeding cerithiopsid gastropod.

MATERIALS AND METHODS

Radulae were removed from preserved specimens by mid-dorsal incision of the buccal cavity after observation of the configuration of the radular ribbon and its relationship to the odontophore. Radulae were cleaned in distilled water after brief immersion in 10% sodium hydroxide to macerate and remove extraneous proteinaceous material. Manipulation of the radulae under low power of a light microscope was used to establish topographic relationships and the range of obvious and easily facilitated mechanical movements of major fields of radular teeth. Radulae were then divided into a series of segments, placed in vials numbered from anterior to posterior, and run through a graded alcohol series from 70 to 100% to remove as much water

as possible prior to drying for scanning electron microscopy.

Some segments were set aside for further examination with light microscopy. The anteriormost segment and segments from the fully formed but unused mid portion of the radula of each species were further cleaned in an ultrasonic cleaner and air dried. In addition, individual teeth and clusters of teeth of different morphologies were cleaned and air dried. Dried radular material was attached to SEM stubs, coated with gold, and examined at low accelerating voltages following procedures outlined by HICKMAN (1981, 1983). Similar preparations were made of radulae of related pleurotomariacean gastropods in the families Scissurellidae and Haliotidae and of a sponge-feeding cerithiopsid mesogastropod of greater phylogenetic distance but similar feeding ecology.

RESULTS

Central Tooth Field

The major features of the pleurotomariid central tooth field are illustrated in Figure 1. Figures 2 and 3 provide comparable illustrations of the central tooth fields of the other two families in the Pleurotomariacea, the Scissurellidae and the Haliotidae. The major characteristics of the pleurotomariid radula are as follows: (1) The teeth in the central field are obscured in the flat-lying excised radula by the larger and more well-developed marginal tooth fields. (2) The teeth in a half row of the central field are arranged with both cusps and bases in a characteristic "V" shape. (3) The number of teeth in the central field (as many as 59) is greater than in any known prosobranch. (4) The central field is asymmetric, and there are a number of distinctive features of the asymmetry: the rachidian tooth is, itself, asymmetric (Figure 4); the teeth within the central complex on either side of the rachidian

have their bases and cusps positioned asymmetrically relative to the mirror plane perpendicular to the plane of the radular ribbon; and the skewing of the asymmetry may be either to the left or the right. It is, for example, right-skewed in *Pleurotomaria* (*Perotrochus*) *quoyana* and left-skewed in *Pleurotomaria* (*Perotrochus*) *midas* (Figures 4 and 5, respectively). This form of asymmetry has evolved independently in a number of prosobranch lineages, as pointed out previously by HICKMAN (1982; 1984). (5) There are three major types of teeth in the central field: the asymmetric rachidian, hooded and irregularly formed inner laterals, and a set of more regularly developed outer laterals that grade from a simple lamellar form to complexly reinforced and cusped. These tooth types are described more fully below.

Rachidian: The rachidian is a narrowly elongate structure that may be irregular in its development, its folded appearance, and the sometimes ragged terminal end. It generally has thin lateral folds that overlap similar lateral folds on the two inner lateral teeth. Although the rachidian tapers distally and may be folded into an acutely pointed terminus, one would not call it a standard cusp, nor is an obvious function suggested.

Inner laterals: The first three or four teeth on either side of the rachidian are similar to the rachidian in their broad, thin, and folded form. The inner pair is the largest, and each has an irregularly enlarged hood-like distal termination that faces away from the rachidian and partially enfolds and covers the terminations of the adjacent and smaller inner lateral teeth. The remaining inner laterals are progressively smaller and with less well-developed hood-like terminations.

Outer laterals: The outer lateral teeth, which have been referred to as "lamellate" by some authors (BARNARD, 1963; FRETTER, 1964, 1966; HYMAN, 1967:237), are com-

Explanation of Figures 1 to 9

Figure 1. *Pleurotomaria* (*Perotrochus*) *quoyana* Fischer & Bernardi, 1856. Rachidian and lateral teeth. University of Miami, Rosenstiel Institute of Marine Science, Gerda Sta. G-897. Bar = 200 μ m.

Figure 2. *Haliotis rufescens* Swainson, 1822. Rachidian, lateral, and inner marginal teeth. University of California, Museum of Paleontology Loc. UCMP R-3200. Bar = 200 μ m.

Figure 3. *Scissurella crispata* (Fleming, 1828). Rachidian, lateral, and inner marginal teeth. R/V Oregon Sta. BMT-9. Bar = 40 μ m.

Figure 4. *Pleurotomaria* (*P.*) *quoyana*. Asymmetric rachidian and skewed lateral tooth rows with right laterals situated farther anterior than corresponding left laterals. Specimen same as Figure 1. Bar = 200 μ m.

Figure 5. *Pleurotomaria* (*P.*) *midas* Bayer, 1965. Asymmetric rachidian and skewed lateral tooth rows with left laterals situ-

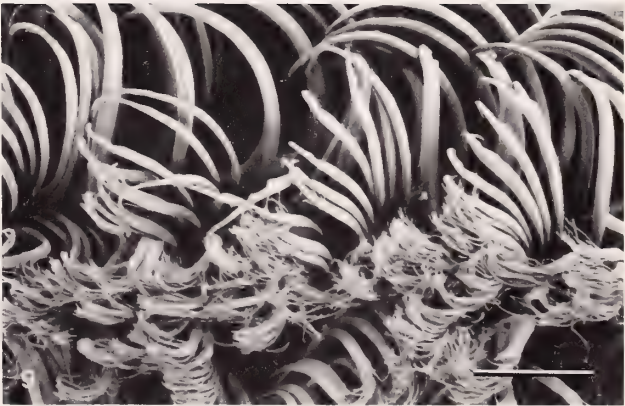
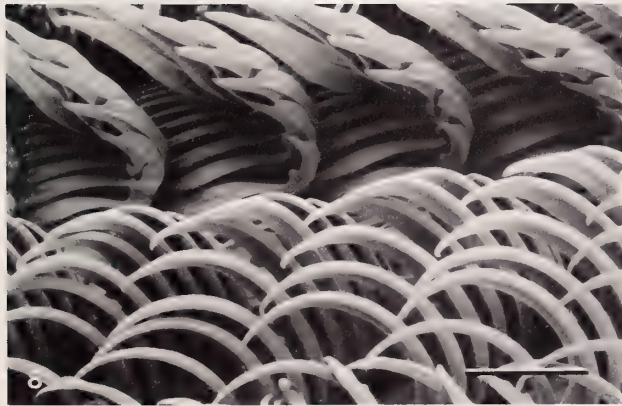
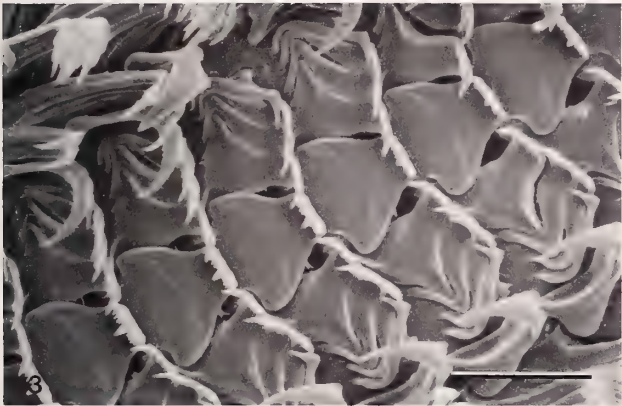
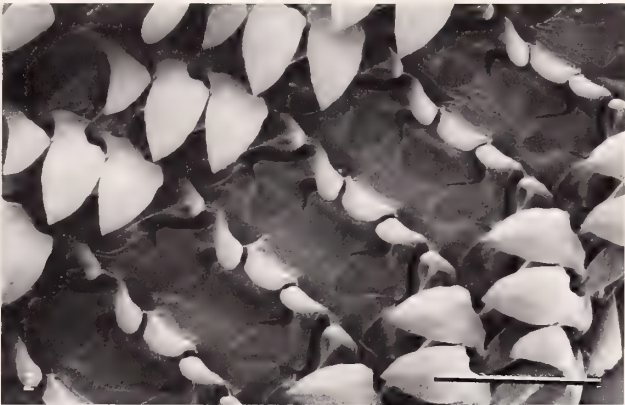
ated farther anterior than corresponding right laterals. University of Miami, Rosenstiel Institute of Marine Science, Gerda Sta. G-10-16. Bar = 500 μ m. Figures 6 to 9 are from the same radula.

Figure 6. Right outer lateral teeth in the region of transition from lamellar plates (on left) to larger teeth with terminal and subterminal denticles (on right). Bar = 400 μ m.

Figure 7. Enlarged view of left outer lateral teeth oriented to show ridges or thickenings on compressional surfaces of cusps. Bar = 200 μ m.

Figure 8. Transition from lateral to marginal teeth. Right outer lateral teeth are above and right inner marginals (sickle teeth) are below. Bar = 400 μ m.

Figure 9. Transition from inner to outer marginals. Right inner marginal sickle teeth are above and right outer marginal filament-tipped teeth are below. Bar = 400 μ m.



plex both in their row configuration and in the morphological gradation within rows. They are numerous (24–26 per half row), and they are arrayed with their bases and cusps forming a “V.” The first 18 to 20 teeth on the inner segment of the “V” are relatively thin lamellar plates, each with a small terminal bend or fold that might be called a cusp. The plates are thickened on their inner margins by enrolling of the edge. At the base, the partially enrolled edge is expanded and attached to the radular membrane in a configuration that should facilitate twisting of the plate and allow more freedom in its movement. The teeth along this segment of the “V” are aligned nearly parallel to the longitudinal axis of the radula rather than in more standard “transverse” rows. When the radula is viewed in cross section, these teeth lie in topographic “gulches,” somewhat lower than the larger and more expanded rachidian and inner laterals, and much lower than the well-developed marginal complexes. At the base of the “V” the outermost laterals begin to increase in length. They are no longer thin, small lamelliform elements, but become complexly reinforced in cross-sectional shape and develop both a terminal and a subterminal pointed denticle. The transition in this region of the radula is illustrated in Figure 6. On the convex or compressional surface of the cusps, thickenings or “compressional ridges” (HICKMAN, 1981) are evident (Figure 7). The form of such teeth implies contact with the substratum during feeding.

Marginal Tooth Fields

The major features of the pleurotomariid marginal tooth fields are several. (1) The most massive and most morphologically complex teeth are found in this portion of the radula rather than in the central tooth field. (2) The cross-sectional shape of the radula and its configuration in the animal relative to the odontophore suggest that the marginal teeth, rather than the central complex, are the major food-preparing structures. (3) The large inner marginal teeth are accommodated in the folded radula in alternating, zipper-like fashion from one side of a row to another.

(4) Three major types of teeth occur in each of the marginal fields: hook-shaped sickle teeth, the filament-tipped tangle teeth, and the paddle-shaped teeth. Each of these types is described below.

Sickle teeth: The innermost marginal teeth are the most formidable teeth in the pleurotomariid radula. Between 11 and 21 of these teeth occur in each half row. Other authors have referred to them as “hooked” teeth (FRETTER, 1964, 1966) or “falcate plates” (BARNARD, 1963; AZUMA, 1964). The abrupt transition from outer laterals to these teeth is illustrated in Figure 8. Although the term “hooked” does accurately portray the fact that the teeth are curved, it does not convey any notion of complex cross-sectional shape. The term “sickle” is a better descriptor not only of curvature, but also of the cross-sectional shape and the distribution of materials. The terminology is not intended to imply close similarity of function, however.

Filament-tipped teeth: The major portion of the marginal tooth complexes consists of so-called brush teeth (FRETTER, 1964, 1966), bristle teeth (HYMAN, 1967), or marginals with “tufts of bristles” (BARNARD, 1963). They have been considered to be unique to the pleurotomariid radula, and they are of a complex form that cannot be described fully using light microscopy and low magnification. There is also a heretofore undocumented discrepancy between the appearance of the morphology before and after use by the animal in feeding. The transition from sickle teeth to filament-tipped teeth is illustrated in Figure 9.

A typical unused but fully formed tooth from the middle of a half row has two types of terminal structures (Figure 10): a group of numerous, thin filaments that lie parallel to one another and, below them, a laterally flattened portion that is deeply notched to form three prominent blunt denticles. The innermost teeth within any half row tend to be more weakly denticulate and lack the filaments, while the outermost teeth lack denticles and the filaments are greatly shortened and reduced in number. The terminal end of a typical tooth is enlarged in Figure 10 to show both types of structure. Figure 11 provides a proximal

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Explanation of Figures 10 to 17

Figure 10. *Pleurotomaria* (*Perotrochus*) *midas* Bayer, 1965. Enlarged tip of a filament-tipped tooth showing filaments and subterminal denticles. Bar = 40 μ m. This figure and Figures 11 to 15 are from the same radula illustrated in Figures 5 to 9.

Figure 11. Filament-tipped tooth showing region in which filaments arise from tooth shaft in parallel series. Bar = 20 μ m.

Figure 12. Detail of the distal end of two filament clusters to show branching of individual filaments. Bar = 10 μ m.

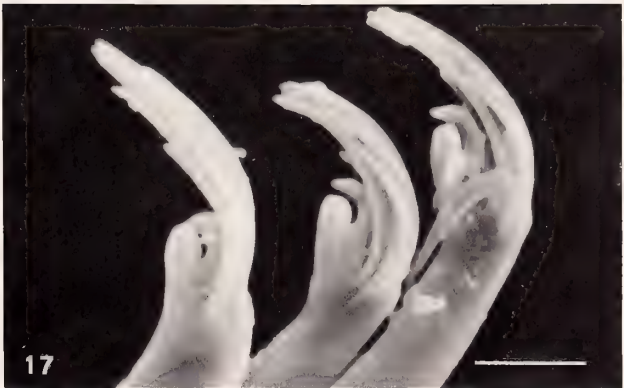
Figure 13. Shafts and terminal filaments viewed from above to show flattening of tooth shafts. Concave surfaces on left face central axis of radula. Bar = 100 μ m.

Figure 14. Region of origination of filament clusters viewed from above to show two series arising one on either side of a central subcylindrical pit. Bar = 20 μ m.

Figure 15. Used filament-tipped teeth from the anterior end of the radula. Bar = 100 μ m.

Figure 16. *Pleurotomaria* (*P.*) *quoyana* Fischer & Bernardi, 1856. Used and worn teeth from anterior end of radula. Bar = 400 μ m.

Figure 17. *Seila terebelloides* (Hutton, 1873). Marginal teeth showing convergent development of terminal filaments and subterminal denticles. University of California, Museum of Paleontology Loc. UCMP D-9044. Bar = 4 μ m.



detail of the pattern by which filaments arise in parallel series from the flattened tooth shaft, while Figure 12 is a detail of the distal end of two filament clusters, showing that each filament may branch four or five times to form a secondary cluster of terminally pointed filaments.

The entire shaft of the tooth is flattened and slightly concavo-convex, as illustrated by viewing the teeth from above (Figure 13). The concave surface is the surface nearest the central axis of the radula, and it is the leading edge in sweeping movements of the teeth. When the region of origination of the filaments is viewed at even higher magnification from above (Figure 14), two parallel series of filaments and a central subcylindrical pit are evident.

Nothing in the appearance of these unworn teeth contravenes the traditional notion of bristliness or mechanical stiffness. However, when they are manipulated while wet, it is clear that they lack flexural stiffness, and examination of teeth from the worn anterior end of the radula of *Pleurotomaria* (*Perotrochus*) *midas* shows the filaments in a tangled disarray that suggests more similarity to a mop than to a broom (Figure 15). However, this particular animal may, shortly before capture, have been radulating a substrate that produced an unusual wear pattern. This pattern has not been reported previously, and teeth from the same region of the radula of a specimen of *P. (P.) quoyana*, although showing evidence of flexibility and wear (Figure 16), are not in the same tangled state.

Paddle-shaped teeth: The final 6 to 10 teeth in each half row of the marginal complex are lacking in both filaments and terminal denticulation. They are flattened and bluntly paddle shaped. Flattened paddle-shaped teeth also occur singly as outermost marginals in some gastropods in the family Trochidae (HICKMAN, 1981), the prosobranch family that appears to be most closely related to pleurotomariids in a number of aspects of morphology and anatomy. The question of whether similarity of form is to be interpreted as indicative of phylogenetic affinity or as convergence related to function will be treated below.

The Radula of *Seila*

The filament-tipped teeth of *Pleurotomaria* have been considered unique among the Gastropoda. Although BARNARD (1963) followed other authors in considering this type of tooth to be characteristically pleurotomariid, he noted a similar morphology portrayed in THIELE's (1929) illustration of the radula of the cerithiopsid genus *Seila* A. Adams, 1861. Drawings in a recent monographic treatment (MARSHALL, 1978) further reinforce the similarity, and a scanning electron micrograph of the analogous tooth from the radula of *Seila terebelloides* (Hutton, 1873) is provided for comparison in Figure 17.

DISCUSSION

Although pleurotomariid gastropods attract considerable attention as collector's items, as objects of great beauty,

and as "living fossils," the foregoing detailed description and illustration are not provided simply to add to the mystique already surrounding these animals. Previously unappreciated morphological features of the radulae of living pleurotomariids provide a basis for reconsidering the function of the morphology and the extent to which morphology is a reflection of heritage from a Paleozoic ancestor that had a primitive gastropod radula.

How Primitive is the Pleurotomariid Radula?

In its anatomy and basic shell form, living *Pleurotomaria* displays many features of gastropod organization that are inferred to be primitive and that have been abandoned in the course of Phanerozoic gastropod evolution. However, neither the long evolutionary history of pleurotomariids nor the conservative evolution of the shell justify concluding that the radula is conservative. In fact, several reasons suggest that the radula is highly specialized and may bear little resemblance to the radulae of ancient Paleozoic pleurotomariaceans.

The first reason for caution is the dissimilarity between the radulae of large, living slit shells and those of scissurellids and haliotids, members of the other two extant pleurotomariacean families (Figures 1 to 3). The evolution of diverse radular morphology within the superfamily shows no shared elements to suggest a unified primitive superfamilial plan that has been resistant to change. The second reason for caution is the difference in ecology separating Paleozoic and Mesozoic pleurotomariaceans from living species (HICKMAN, 1976). The early fossil record of slit shells occurs predominantly in shallow-water deposits, where shells are found in association with reef-building and reef-inhabiting organisms. The living slit shells, on the other hand, are restricted to relatively deep water and rocky substrates. The encrusting invertebrates with which *Pleurotomaria* has been observed and the presence of abundant sponge spicules in the gut suggest an unusual form of "grazing" and source of nourishment. The large number of teeth per transverse row in the radula of *Pleurotomaria* is frequently cited as a primitive feature (HYMAN, 1967:236). It can be generalized that prosobranch evolution, as inferred from features other than the radula, is accompanied by progressive reduction in the numbers of teeth per row and the number of different kinds of teeth in the radula. It would be unwarranted to reject the possibility that some features of the *Pleurotomaria* radula are conservative; but it seems unlikely that, in morphological detail, we are glimpsing a feeding organ preserved from the Paleozoic era.

To What Extent Does Pleurotomariid Radular Morphology Reflect Function?

If radular morphology in the Pleurotomariidae has not been constrained closely by a plan that could not be changed readily, we can assume that some of the variation

and complex form has evolved either as mechanical alteration of the apparatus or as solutions to problems of preparing and ingesting particular kinds of food resources. It is tempting to conclude that many of the unusual features of the radula are adaptations for sponge feeding, but demonstrations of how an apparatus works and how efficiently it works go beyond the trivial observation that it does work.

Without knowing anything about the properties of the substrates on which the apparatus is used, little can be concluded about the suitability of design for preparing and gathering food. However, a number of features are subject to mechanical interpretation (*sensu* HICKMAN, 1981).

The topological arrangement and the irregular and underdeveloped morphology of elements in the central field both suggest that the central field acts mechanically to separate the marginal fields rather than to actively prepare and gather food. The asymmetry of the central field and its facilitation of alternatively interleaved accommodation of the rows of large sickle-shaped inner marginals further suggest a predominantly (not necessarily exclusively) non-feeding function for the central complex. Features such as compressional ridges on the outermost lateral teeth and the pattern of distribution of materials in the sickle-shaped teeth, as well as the concavo-convex cross-sectional shape of the shafts of the filament-tipped teeth, suggest mechanisms for dealing with different forms of stress. They are similar in form to engineering solutions to dealing with stress in man-made structures or implements.

Mechanical behavior of materials, such as the flexibility of filaments in the radular elements previously called "bristle" teeth, limits the possible range of functions. Finding these filaments in tangled disarray in the anteriormost portion of the radula demonstrates their flexibility and suggests that their function is not one requiring great flexural stiffness.

The bristle-like appearance of the distal end of the newly formed teeth provides a lesson in the analysis of morphology and the constraints on form (HICKMAN, 1981). The newly formed appearance of this particular morphology may not be providing us with information about phylogenetic or adaptive functional constraints so much as it is providing information about constructional constraints on how the building material can be secreted. Chitin can be secreted as separate fine filaments, but the filaments will be secreted in parallel rather than in the disarrayed configuration in which they are subsequently used.

Morphological Convergence in *Pleurotomaria* and *Seila*

The strongest argument for a functional interpretation of the pleurotomariid filament-tipped teeth as adaptations to sponge feeding and the strongest argument against their

interpretation as phylogenetically constrained conservative morphology is the appearance of remarkably similar teeth in the radula of sponge-feeding mesogastropods of the genus *Seila*. These observations do not confirm how the morphology is used, nor do they establish optimality of design; but the inference that selection has been operative is strong.

CONCLUSIONS

Interpretation of the unusual radular morphology of living pleurotomariid gastropods requires consideration of the alternative constraints of the long and conservative phylogenetic history of the superfamily, the mechanics of an apparatus that moves and deals with stress, the ecological factors involved in interaction of the apparatus with specific feeding substrates, the limitations of the material from which the apparatus is constructed, and the developmental limitations on how the material can be used to form individual teeth with fine morphological detail.

Several lines of evidence suggest that the radula of *Pleurotomaria* is not morphologically conservative or closely constrained phylogenetically and that it should not be taken as a representation of the primitive gastropod radula. The evolutionary results of mechanical constraints are visible primarily in the distribution of materials in individual teeth, particularly in cross-sectional shapes. Those teeth constructed to deal most effectively with stress are situated in the marginal tooth complexes rather than in the central complex, although it is in the innermost portions of the marginal complexes that most of the forces are apparently generated.

Demonstration of the flexibility of the elements formerly referred to as "bristles" requires an alternative interpretation of their mechanical function in feeding. Although sponge material has been reported as common in the gut contents of slit shells, it cannot be argued from morphology alone that the flexible filaments represent an adaptation for sponge feeding. The most powerful evidence that morphology is related to sponge feeding comes from the independent development of similar morphology in an unrelated group of sponge-feeding mesogastropods.

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The Pleurobranchidae (Opisthobranchia: Notaspidea) of the Marshall Islands, Central-West Pacific Ocean

by

R. C. WILLAN

Department of Zoology, University of Queensland, St. Lucia,
Brisbane, Queensland 4067, Australia

Abstract. The following pleurobranchs were identified in a collection made by Mr. Scott Johnson at Enewetak Atoll, Marshall Islands, central-west Pacific Ocean: *Berthellina citrina* (Rüppell & Leuckart, 1828); *Pleurehdera haraldi* Marcus & Marcus, 1970; *Berthella pellucida* (Pease, 1860); and *Berthella martensi* (Pilsbry, 1896). This material represents significant range extensions for *P. haraldi* and *B. martensi*, the former known previously from only the unique holotype and the latter "lost" for over a century. The Pleurobranchidae shows much greater intraspecific variation in sculpture of the jaws' elements than had previously been suspected.

INTRODUCTION

WHILE stationed at the Mid-Pacific Research Laboratory on Enewetak Atoll, Marshall Islands, central-west Pacific Ocean, Mr. Scott Johnson made extensive collections of opisthobranchs. He generously sent me the side-gilled sea slugs (Pleurobranchidae) he collected and photographed on research sorties and longer residences between 1975 and 1983.

The collection, which totals 21 specimens and 14 color transparencies, is interesting for two reasons. First, it provides material from the largely unsampled, tropical, central Pacific region. Secondly, "large" pleurobranchs—i.e., species of *Pleurobranchus* in excess of 60 mm crawling length as adults (such as *P. grandis* Pease, 1868, *P. mamillatus* Quoy & Gaimard, 1832, *P. forskali* Rüppell & Leuckart, 1828, and *P. peronii* Cuvier, 1804)—which would have been expected to be present, are inexplicably lacking, as are members of the subfamily Pleurobranchaeinae (e.g., *Euselenops luniceps* (Cuvier, 1817) and *Pleurobranchaea* spp.).

The collection consists of the following four species, all of which belong to the subfamily Pleurobranchinae:

Berthellina citrina (Rüppell & Leuckart, 1828)
Pleurehdera haraldi Marcus & Marcus, 1970
Berthella pellucida (Pease, 1860)
Berthella martensi (Pilsbry, 1896).

MARCUS & BURCH (1965) described 15 species of opisthobranchs from Enewetak Atoll collected by Dr. J. B.

Burch in 1960, but there were no pleurobranchs in that collection.

TAXONOMY

Berthellina citrina
(Rüppell & Leuckart, 1828)

(Figures 33 to 36)

Synonymy

BURN (1962) has given an extensive synonymy for this widespread Indo-Pacific species. WILLAN (1983) added three more synonyms: *Pleurobranchus cuvieri* Bergh, 1898; *Berthella borneensis* Bergh, 1905; and *Berthella minor* Bergh, 1905. In addition, it would seem that *Pleurobranchus rufus* Pease, 1860, with type locality of Hawaii, is another synonym. The original description (PEASE, 1860) gave a brief statement of external features only, but the clues to its identity are there. *Pleurobranchus rufus* was described as having a "smooth" body, "uniform vermilion" color and a length of "1 inch." No other Hawaiian pleurobranch possesses all three characters. The presence of *Berthellina citrina* in Hawaii has been verified by KAY (1979) and BERTSCH & JOHNSON (1981).

I am not prepared to admit *Berthellina engeli* Gardiner, 1936, into the synonymy of *B. citrina* as EDMUNDS & THOMPSON (1972) have done.

Material

- (1) 2 specimens (15, 14 mm long preserved) from under dead coral, 1 m, Bokandretok Reef, Enewetak Atoll. S. Johnson, 22 May 1982.

- (2) 2 color transparencies of a specimen (22 mm extended crawling length), from under dead coral, 10 m, Sand Island Pinnacle, Enewetak Atoll. S. Johnson, 19 July 1982.
- (3) 2 specimens (16, 14 mm extended crawling length), from under dead coral, 10 m, Sand Island Pinnacle No. 2, Enewetak Atoll. S. Johnson, 5 March 1983.

Description

These Marshall Islands specimens agree well with *Berthellina citrina* from elsewhere in the Pacific Ocean (see WILLAN, 1983). The body is apricot with a very few white specks; its transparency allows the reddish-golden shell to be seen through the mantle anteriorly and the black digestive gland posteriorly. The gill is longer and more narrow than in *Berthella* species, and it has a smooth rachis. The two Bokandretok Reef specimens had 22 and 18 pinnae on the dorsal side of their gill raches respectively.

The radula is large, broad, and relatively elongate. Formulae are $85 \times 186.0.186$ and $75 \times 130.0.130$ respectively. All the teeth are very elongate with 15 to 20 denticles on the posterior face of the blade; the middle lateral teeth are longest. The jaws (Figure 35) are relatively elongate. The mandibular elements, when viewed at the surface of the jaw (Figure 36), are noticeably elongate (60–70 μm long and 30–35 μm wide). Every one is smooth-bladed.

The reproductive system is identical to that described by BURN (1962) and WILLAN (1983) for Australian and New Zealand specimens respectively.

Abundance

Mr. Johnson has seen 24 specimens of *Berthellina citrina* at Enewetak Atoll. Most were beneath dead coral blocks on lagoon pinnacles and on the seaward reef slope at depths of 8 to 15 m. Two specimens have also been observed at Kwajalein Atoll on a southern lagoon pinnacle.

Pleurehdera haraldi Marcus & Marcus, 1970

(Figures 1 to 5, 13 to 16, 19, and 20)

Synonymy

Pleurehdera haraldi MARCUS & MARCUS, 1970:158–160, figs. 8–10.

Material

- (1) 1 specimen (40 mm extended crawling length) and color transparency, from under dead coral, 3 m, Enewetak Island, Enewetak Atoll. S. Johnson, 25 Nov. 1981.
- (2) 1 specimen (14 mm extended crawling length), from under dead coral, 4 m, Lagoonside, Enewetak Island, Enewetak Atoll. S. Johnson, 11 Dec. 1981.
- (3) 1 specimen (18 mm extended crawling length), from under dead coral, 5 m, Lagoonside, Enewetak Island, Enewetak Atoll. S. Johnson, 19 May 1982.
- (4) 2 color transparencies of a specimen (30 mm extended crawling length), from under dead coral, 10 m, Ikuren Island, Enewetak Atoll. S. Johnson, Sept. 1981.
- (5) 3 specimens (25, 10, and 6 mm extended crawling length), from under dead coral, 5 m, Lagoonside, Enewetak Island, Enewetak Atoll. S. Johnson, 16 May 1982.
- (6) 2 specimens (24, 20 mm extended crawling length), from under dead coral, 5 m, Lagoonside, Enewetak Island, Enewetak Atoll. S. Johnson, 14 July 1982.
- (7) 2 specimens (both 22 mm extended crawling length) and two color transparencies, from under dead coral, 2 m, Lujor Channel, Enewetak Atoll. S. Johnson, Sept. 1981.

Mr. Johnson also kindly sent a transparency of a living specimen from Hawaii (taken at night in a cave, 12 m, Pupukea, Oahu, August 1980).

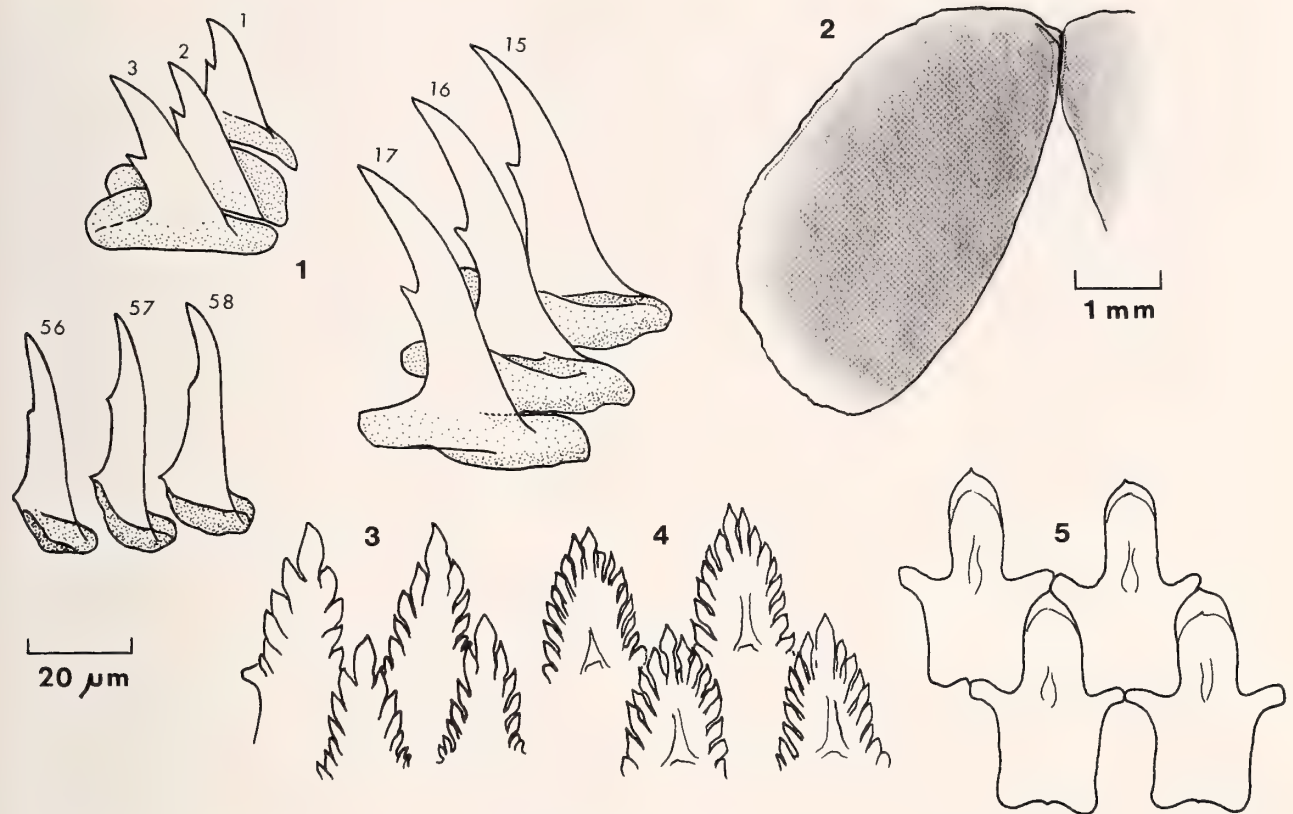
Description

Pleurehdera haraldi was previously known from only the unique holotype that was preserved when described. A full account is given here to relate the features of the living animal and to present additional data pertinent to its important place in pleurobranch phylogeny (MARCUS & MARCUS, 1970; WILLAN, 1983).

Living specimens can reach 40 mm in length when extended and crawling actively. In this state (Figure 14) the mantle is elongate-oval with lateral indentations. The anterior mantle border is entire not emarginate. The oral veil and rhinophores project in front of the anterior margin of the mantle (in fact the region of fusion of the rhinophores is visible in advance of the mantle). The oral veil is wide, its lateral edges diverging widely and being noticeably tentaculate; the anterior margin is smooth and gently undulating, without any indication of a mid-anterior embayment. The rhinophores are short, broad, and extend outwards rather than curving upwards.

In life the mantle's appearance and texture resemble those of *Berthellina citrina*. The mantle is soft and wrinkled, and extends beyond the foot a considerable distance laterally and posteriorly—hence it covers the gill at all times. Its edges are thin. The mantle's surface is smooth, yet magnification reveals numerous, tiny pores. The mantle has a characteristic texture in preserved animals: it is rough and honeycombed (this honeycombing is visible without magnification). The undersurface has a fibrous, sponge-like texture. By contrast, the mantle of *Berthellina citrina*, when preserved, is smooth and textured like velvet.

The living animal has a translucent body with a flush of pale pink, fawn, or brown; when a specimen is resting, the mantle becomes wrinkled and the folds between the wrinkles are darker brown. The mantle's translucency permits the viscera (particularly the creamish-orange ovotestis and black digestive gland) to be seen easily. The



Explanation of Figures 1 to 5

Radula and jaws of *Pleurehdera haraldi*. Figure 1. Inner, middle, and outer lateral teeth. Figure 2. Entire right jaw laid flat showing inner surface. Figures 3, 4, 5. Detail of mandibular elements from same region on inner face of jaws of three different specimens. Figures 1, 3, 4, and 5 are drawn to same scale.

mantle has a scattering of small, intense, opaque white spots over its entire surface and more numerous, smaller gray speckles. Never was a differently colored marginal zone present on the mantle. The rhinophores, oral veil, and foot are translucent white or tan. The gill can be either translucent white or whitish with faint brown speckling. The genital apertures are white. Not one of the specimens had been sufficiently well fixed to enable discernment of a pedal gland. Neither could the number of gill pinnae be counted. However, the gill does have a smooth rachis and is free from the body for approximately half its length. The anus opens on the dorsal side of the gill at the hind end of the basement membrane.

The shell is relatively small (one-third adult body length) and exceedingly thin, although it is calcified. It is situated anteriorly above the viscera as in *Berthellina*. One specimen had no shell. The shells of the other two Marshall Islands specimens matched the description of MARCUS & MARCUS (1970).

The radula is nearly square. Radulae from three specimens were stained, mounted, and examined. The Enewetak Island specimen (collected 25 Nov. 1981) was 17 mm long preserved; its radula measured 2.3 mm long by 1.8 mm wide when flattened on a slide; and its radular for-

mula was $59 \times 73.0.73$. The Enewetak Island specimen (collected 11 Dec. 1981) was 12 mm long preserved; its radula measured 1.6 by 1.2 mm; and its radular formula was $54 \times 60.0.60$. Another Enewetak Island specimen (collected 19 May 1982) was 11.5 mm long preserved; its radula measured 1.9 by 1.7 mm; and its radular formula was $54 \times 67.0.67$.

The innermost lateral teeth have a long basal plate and a broad, curving, almost triangular main cusp (25 μ m in vertical height) with a strong accessory denticle on the outer face. The denticle, which is 9 μ m in vertical height, arises from the main cusp, never directly from the basal plate. The lateral teeth increase progressively in size, with the fourth and successive teeth being larger and straighter than the innermost three teeth. The middle laterals are tall and erect (110 μ m vertical height) and still have a conspicuous denticle. The outermost laterals are narrow and almost as tall as the middle laterals (95–110 μ m vertical height); most clearly show a small denticle or projecting angle on the outer face. The presence of a single accessory denticle on all teeth is one of the unique features of *Pleurehdera haraldi*.

The jaws are ovate, rather small (each measuring 4.1 mm long by 1.7 mm wide in the 12 mm Enewetak Island

specimen) and particularly thin along the dorsal margin and posterior end (Figure 2). The mandibular elements are cruciform, each having an elongate, parallel-sided blade with a definite projection mid-way along the element (*i.e.*, at the base of the blade). Two specimens had denticulate blades (Figures 3, 4, 19, and 20) and one had smooth blades on its mandibular elements (Figure 5) (see Remarks section under *Berthella pellucida* for a discussion of the significance of smooth or denticulate blades). The smooth-bladed elements are the same size (41–45 μm vertical height) as the denticulate elements (35–38 μm ; 42–46 μm). The two specimens with denticulate edges both have elongate blades; the blades carry four to six denticles in one, and six to seven denticles in the other specimen. The denticles are narrow and forward-pointing and lack apical thickenings. Because of the intraspecific variation in mandibular element morphology, I have illustrated elements from each specimen (Figures 3 to 5).

The reproductive system of the only mature individual (the 40 mm Enewetak Island specimen) was too badly fixed to allow examination of any details.

Abundance

Mr. Johnson has recorded 18 specimens of *Pleurehdera haraldi* from Enewetak Atoll. Most were observed on shallow inshore reefs beneath dead coral at depths of 3 to 6 m. One specimen was observed in a similar habitat at Bikini Atoll. The single specimen from Hawaii (for which only a slide was available) was found at a depth of 12 m.

Remarks

The recognition of *Pleurehdera haraldi* from the Marshall Islands and Hawaii represents significant range extensions outwards from the Tuamotu Archipelago where it was first described (MARCUS & MARCUS, 1970), and indicates that the species occurs throughout the tropical, central Pacific Ocean.

The specimens examined by me agree well with the holotype in most features (*i.e.*, size, mantle, gill rachis, shell, anal position, mandibular elements, and radula). They differ only in color. The Marcuses' specimen was reported (on the basis of preserved material only) as black all over (the darkly-pigmented epithelium was able to be rubbed off) with a narrow, white marginal line. My specimens, which were accompanied by color notes made from life and by photographs, were translucent pale pink or brown with white specks on the mantle. I cannot explain the differences in color.

The present material allows an appraisal of the taxonomic position of *Pleurehdera* within the Pleurobranchidae. It is undoubtedly a unique genus because of characters of its mantle, foot, shell, radula, and mandibular elements. MARCUS & MARCUS (1970:159) felt *Pleurehdera* reduced the gap between the Pleurobranchinae and the Pleurobranchaeinae because they found so much vari-

ability between the elements on the jaws of their one specimen. While acknowledging that there is considerable intraspecific variability in the mandibular elements, even more than originally appreciated (see Figures 3 to 5), I find all the elements to be of the cruciform type (*i.e.*, elongate in shape with lateral projections at the base of the blade) rather than polygonal. As such, they do not resemble the elements of *Pleurobranchaea* or *Bathyberthella*. Thus, *Pleurehdera* should be firmly located in the subfamily Pleurobranchinae. This is where the Marcuses put it. In fact, it is closer to *Berthellina* than to *Berthella*, *Bathyberthella* or *Pleurobranchus* because of its mantle texture, small anteriorly located shell, and denticulate radula (with denticulation confined to one denticle per tooth). Therefore, if one follows the BURN (1962) scheme of classification for the Pleurobranchidae (as explained by WILAN, 1983), *Pleurehdera* belongs to the berthelline group.

Berthella pellucida (Pease, 1860)

(Figures 6, 7, 17, 18, 29, 37 to 39, and 44)

Synonymy

Pleurobranchus pellucidus PEASE, 1860:24; PILSBRY, 1896:203, 204; BERGH, 1898:119; VAYSSIÈRE, 1898:343; RISBEC, 1928: 63–66, figs. 79–87; BABA, 1969:190, 191, fig. 1.

Berthella postrema BURN, 1962:140–142, pl. 1, fig. 2, pl. 2, figs. 3–4, text figs. 1b, 2b, 4.

Berthella pellucida Pease; THOMPSON, 1970:188, fig. 8; KAY, 1979:443.

Material

- (1) 2 specimens (16 mm, 12 mm extended crawling length) and color transparency, from under dead coral, 2 m, Enewetak Island, Enewetak Atoll. S. Johnson, 19 Sept. 1982.
- (2) 1 specimen (14 mm extended crawling length) and color transparency, from under dead coral, 8 m, inter-island reef between Bokandretok and Madren Islands, Enewetak Atoll. S. Johnson, 19 Nov. 1982. (Subsequently referred to as Bokandretok/Madren reef specimen.)

Description

The Marshall Islands lie within the tropical, central Pacific range already known for *Berthella pellucida*, *i.e.* from Hawaii (PEASE, 1860; KAY, 1979) to New Caledonia (RISBEC, 1928) and eastern Australia (BURN, 1962; THOMPSON, 1970). I have additional records of this pleurobranch from Moreton Bay of southern Queensland (11 specimens, collected live), Cockburn Sound of Western Australia (photograph courtesy N. Coleman), and Guam (photograph courtesy R. Burn).

The three Marshall Islands specimens agree well with other described *Berthella pellucida*. The 14 mm juvenile from Bokandretok/Madren reef is depicted in Figure 17. The mantle of *B. pellucida* is translucent and pale honey-

brown. Juveniles have a more-or-less distinct, central, vivid, opaque-white cross with white flecks and spots. Adults have only a few, tiny white specks. The mantle is obviously covered with pores and glands over its entire surface, imparting a texture that, in both the living and preserved states, is honeycombed or "waffle-like" (RISBEC, 1928). These pores are visible to the naked eye and are distinct with even low magnification. The anterior edge of the ample mantle is not emarginate; its edges are thin. The gill never protrudes beyond the mantle margin, but it can be seen easily through the transparent mantle. The Bokandretok/Madren reef specimen had 12 pinnae on the upper side of its gill, the rachis of which was smooth. The anus opens at the hind end of the gill membrane.

The shell (Figure 29) is large, almost as big as the mantle (*i.e.*, four-fifths of the preserved body length), convex, and auriculate. The posterior rim is higher than the protoconch. Both the anterior and posterior margins are evenly rounded. The left and right margins are nearly parallel, and there is a distinct shoulder on the left side of the shell. The sculpture is of smooth, concentric ridges present both externally and internally. The shell appears to have a continuous periostracal extension beyond the calcified margin all round.

The radula is small, elongate, rectangular, and not greatly expanded toward the growing end. Radulae from two specimens were stained and mounted on slides; that of the third was coated and mounted on a stub for SEM study. The larger Enewetak Island specimen was 7.5 mm long preserved; its radula measured 1.1 mm long by 0.8 mm wide when flattened on a slide; and its radular formula was $57 \times 55.0.55$. The smaller Enewetak Island specimen, whose radula was examined by SEM, was 6 mm long preserved, and its radular formula was $60 \times 45.0.45$. The Bokandretok/Madren reef specimen was 8 mm long preserved; its radula measured 1.6 mm by 1.0 mm; and its radular formula was $61 \times 58.0.58$ (sizes for teeth given below relate to this radula).

The teeth are numerous and small. The innermost laterals (Figure 37) have a small cusp that is sharply curved toward the growing end of the radula. Innermost laterals measure $12 \mu\text{m}$ in vertical height, and their broad basal plates measure $20 \mu\text{m}$ in length. Beyond the fifth lateral, the middle laterals (Figure 38) increase progressively in size, their cusps become broader and more erect (to $22 \mu\text{m}$ high), and their basal plates are rectangular. Beyond two-thirds of the way across the radula, the middle laterals grade into outer laterals. The outer laterals (Figure 39) are narrow and taller (up to $30 \mu\text{m}$ high); some have a hooked cusp and others are simple pegs; all have small, oval basal plates ($14 \mu\text{m}$ and shorter in length).

The jaws are small, each measuring 1.4 mm by 0.75 mm in the Bokandretok/Madren reef specimen, which was 8 mm long preserved. Their shape is characteristic (Figure 6); they are ovate, the inner margin being perfectly straight and the dorsal (or outer) margin evenly

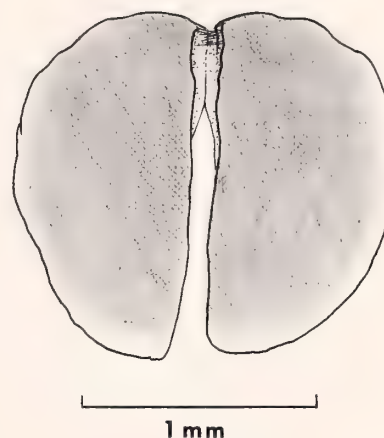


Figure 6

Both jaws of *Berthella pellucida* separated and laid flat showing inner surface.

convex, describing a semicircle. The two jaws are attached to each other anteriorly for approximately one-third of their length. The mandibular elements are cruciform and broad. All three specimens have smooth-sided blades sometimes with thickened (either smooth or coarsely sculptured) edges. The apices are not thickened. A short, mid-central ridge is present on most of the elements. The elements range in height from 38 to $40 \mu\text{m}$. They are rather broad, measuring 20 – $25 \mu\text{m}$ between the lateral projections. When examined with the SEM under high magnification ($\times 5000$), a fine, superficial, shagreened sculpture was noted on all the elements (Figure 44).

The reproductive systems of all the Marshall Islands specimens were immature and too poorly fixed to permit examination of details. Therefore, I studied the reproductive systems of three specimens, collected by myself in southern Queensland (Figure 7). In all animals I found a receptaculum seminis diverging on a short duct directly from the base of the bursa copulatrix. The presence of two allosperm receptacles contradicts BURN's (1962) statement regarding the number of these organs. Also, and most unusually for a species of *Berthella*, the vas deferens was dilated and spongy for a distance along its mid-length. This region comprises a distinct prostate gland. The penial gland is tubular and elongate, and its blind end curves around the base of the bursa copulatrix.

Abundance

Berthella pellucida is the commonest pleurobranch at Enewetak Atoll. Mr. Johnson reports 24 recorded observations plus numerous unrecorded sightings. Nearly all of the animals were on shallow, inshore, protected lagoon reefs between the intertidal zone and 5 m. *Berthella pellucida* has been seen throughout the year and is frequently accompanied by its spawn.

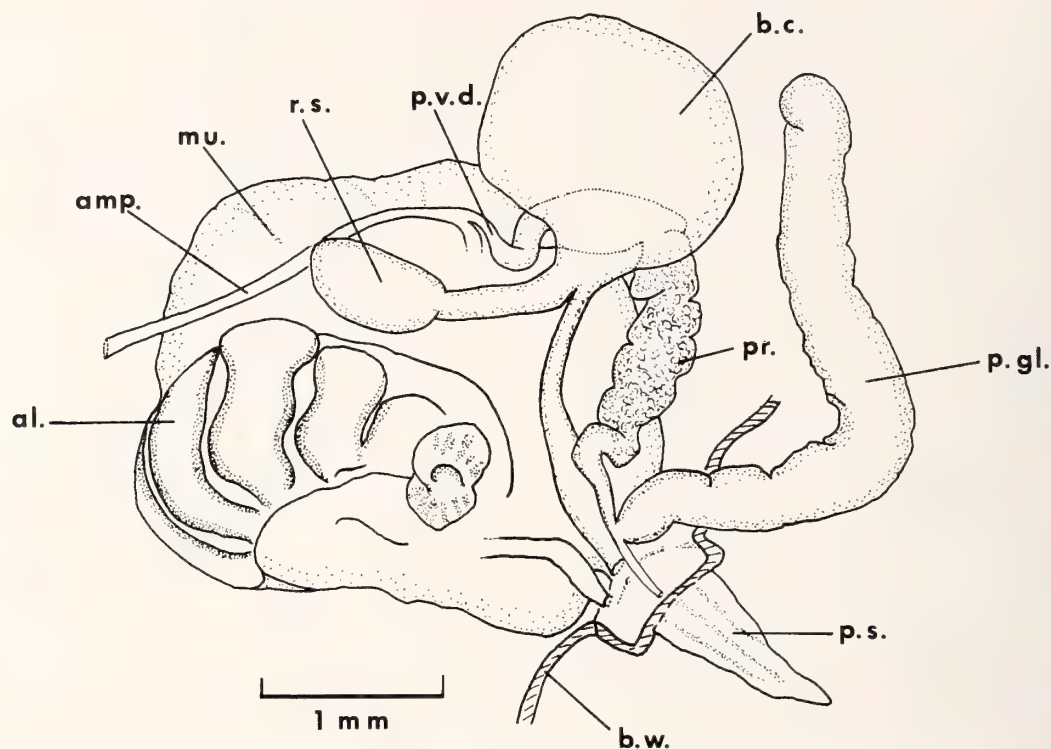


Figure 7

Composite view of structure of reproductive organs of a mature *Berthella pellucida*. Abbreviations: amp., ampullar region of hermaphrodite duct; al., albumen gland; b.c., bursa copulatrix; b.w., cut body wall; p.gl., penial gland; pr., prostate gland; p.s., penial sheath; p.v.d., short proximal section of vas deferens; mu., mucus gland; r.s., receptaculum seminis.

Remarks

BURN's (1962) description of *Berthella postrema* is sufficiently detailed to be sure that that taxon is a synonym of *B. pellucida*. Twelve additional specimens from eastern Australia confirm this view by the match of their appearance, color, radula, and jaw details with Burn's description. As noted above, however, I found differences in the reproductive organs.

The most distinctive features of *Berthella pellucida* are the following: its pale lemon-yellow color with overlay of a white cross or specks; translucent mantle with porous texture; 10 to 14 pinnae on a rather small gill; large, auriculate shell covering the whole of the viscera; anus opening at the hind end of the gill membrane; and broad mandibular elements. The simple radular teeth are like those of other *Berthella* species (e.g., *B. ornata* and *B. mediatas*). The number of pinnae on the gill is less than that for other *Berthella* species. Some details of the reproductive system are typical of *Berthella*, i.e., the origin of the receptaculum seminis off the base of the bursa copulatrix far up the vagina. The enlarged prostatic section of the vas deferens is atypical of *Berthella*.

The mandibular elements are smooth-bladed in all three

Marshall Islands specimens, yet descriptions of *Berthella pellucida* from elsewhere cite them as denticulate (BURN, 1962; THOMPSON, 1970; personal observations of four southern Queensland specimens). This anomaly in important details of mandibular sculpture led me to review the literature closely, and I discovered no less than eight species of pleurobranchs that sometimes possess or sometimes lack denticles to the blades on their mandibular elements. These data are crucial for their bearing on pleurobranch systematics, particularly for the interpretation of species, so I have listed all the examples.

Berthella tupala Marcus, 1957

Reported to have two or three rounded cusps (MARCUS, 1957), zero to five denticles (MARCUS & MARCUS, 1967), or smooth blades (BERTSCH, 1975).

Berthella californica Dall, 1900

Reported to have entirely smooth blades (BERGH, 1905; MACFARLAND, 1966). MACFARLAND (1966) segregated, as a new subspecies (*denticulatus*), animals with one to five, strong, pointed denticles on their elements; yet, *denticulatus* does not differ in other external or internal features. MACFARLAND remarked (1966:84): "In all external

characters it [*Pleurobranchus californicus denticulatus*] coincides with *Pleurobranchus californicus* herein described.”

Berthella ornata (Cheeseman, 1878)

Mandibular blades are normally smooth, but rarely a weak denticle is present on the side of the blade about half way between the lateral projection and apex (WILLAN, 1975, 1983).

Berthella mediatas Burn, 1962

Reported to have three to five strong, coarse denticles (BERGH, 1900; WILLAN, 1975, 1983) or to have edges of blades coarsely roughened, but not noticeably denticulate (BURN, 1962). Two specimens from New Zealand's South Island had irregularly roughened, but certainly not denticulate, blades.

Berthella pellucida (Pease, 1860)

Reported to have two or three strong denticles (RISBEC, 1928; BURN, 1962; present observations of four southern Queensland specimens) or two short denticles on blades (THOMPSON, 1970). The Marshall Islands specimens described herein had smooth-sided blades (Figure 44).

Berthella martensi (Pilsbry, 1896)

VAYSSIÈRE (1898:300) reported two to three small denticles on the blades of the mandibular elements. The elements of all seven specimens I examined had smooth blades (Figure 27), except for one jaw that had a few rows of elements near the outer margin with one to three irregular denticles flanking the cusp (Figure 28).

Pleurehdera haraldi Marcus & Marcus, 1970

MARCUS & MARCUS (1970) noted and illustrated the variation between elements depending on their position on the jaw. Their illustrations show four to ten denticles, which are coarse and strong where there are few, or fine where there are many denticles on the blades. Two of the Marshall Islands specimens reported herein had denticulate blades (Figures 3 and 4) and one had smooth blades (Figure 5).

Berthellina citrina (Rüppell & Leuckart, 1828)

Usually reported to have smooth blades (*e.g.*, BURN, 1962; WILLAN, 1983), THOMPSON (1970) found one or two short, pointed denticles on the blades. WILLAN (1983) gave a SEM of mandibular elements possessing a single, asymmetric cusp.

These eight examples confirm the great degree of intraspecific variation in the sculpture of mandibular elements in the Pleurobranchidae. Until now sculptural details have been interpreted as having high diagnostic significance (*e.g.*, BURN, 1962; MACFARLAND, 1966; WILLAN, 1983). While intra-individual variation in sculpture between elements on one particular jaw has been acknowledged (O'DONOGHUE, 1929:58; PRUVOT-FOL, 1934:32; MARCUS & MARCUS, 1970:159), the potential range of intraspecific variation in sculpture (from completely smooth to strongly denticulate) in some “berthelline”

species has never been suspected. The variation appears to be continuous rather than discontinuous. Such variation cannot be ontogenetic (MARCUS & MARCUS, 1958:21, MACFARLAND, 1966:79, pl. 14, figs. 10–14, and BERTSCH, 1975, have described the development of pleurobranch mandibular elements) nor geographic (see the data for *Berthella mediatas* and *Pleurehdera haraldi* presented above); nor can it be due to a possible artifact or error of preparation or observation on the anatomist's part. The conclusion seems inescapable that many of the small “berthelline” pleurobranchs can have blades to their mandibular elements that are sometimes smooth or sometimes denticulate. Therefore, all researchers should give sculptural details of the mandibular elements less weighting when they are assessing their species against others.

Berthella martensi (Pilsbry, 1896)

(Figures 8 to 12, 21 to 28, 30 to 32, 40 to 42, and 44)

Synonymy

Pleurobranchus scutatus MARTENS in MÖBIUS, 1880:309, pl. 21, fig. 8 (non *Pleurobranchus scutatus* Forbes, 1844).

Bouvieria scutata MARTENS in MÖBIUS; VAYSSIÈRE, 1896:123, pl. 5, figs. 16–18; VAYSSIÈRE, 1898:297, pl. 18, figs. 44–49 (non *Pleurobranchus scutatus* Forbes, 1844).

Gymnotoplax martensi PILSBRY, 1896:211, pl. 48, figs. 34–35; MARCUS, 1977:418; WILLAN, 1978:339, 342.

Material

- (1) 1 specimen (18 mm extended crawling length) and color transparency, from under dead coral, 5 m, Lagoonside, Enewetak Island, Enewetak Atoll. L. Boucher, 26 Jan. 1982.
- (2) 1 specimen (25 mm extended crawling length), from under dead coral, 10 m, Jedrol Island, Enewetak Atoll. S. Johnson, 23 April 1982.
- (3) 1 specimen (12 mm extended crawling length) and color transparency, from under dead coral, 10 m, No Bull Pinnacle Number 2, Enewetak Atoll. S. Johnson, 27 Oct. 1982.
- (4) 1 specimen (30 mm extended crawling length) and color transparency, from under dead coral, 4 m, No Bull Pinnacle Number 2, Enewetak Atoll. S. Johnson, 27 Oct. 1982.
- (5) 1 color transparency of a specimen (23 mm extended crawling length), from 4 m, Enewetak Island, Enewetak Atoll. S. Johnson, 10 Sept. 1981.
- (6) 1 color transparency of a specimen (27 mm extended crawling length), from 2 m, Jinimi Island, Enewetak Atoll. S. Johnson, 23 July 1981.

Mr. Johnson also kindly sent two specimens from Hawaii. They were found crawling in a cave at night, 10 m, Puako, Hawaii, 24 Oct. 1980. Mr. Johnson supplied me with data for sightings of 18 additional live specimens from Hawaii, all at night in 8 to 10 m of water (photographs of two of these were inspected).

I have personally collected two specimens of *Berthella martensi*, at Lizard Island, northern Queensland (1 specimen, 9 Oct. 1982) and N.W. of Point Lookout, southern Queensland (1 specimen, 25 March 1983). Additional photographic records are available from the following localities: Mana Island, Fiji, 1979 (courtesy of Dr. P. Morse); and Fremantle, Western Australia, 1976 (courtesy of Mr. N. Coleman). An excellent color photograph of a specimen from Lizard Island, northern Queensland, has been published by KUITER (1982:37). JOHNSON (1982) has published a photograph of *Berthella martensi* from Hawaii.

Description

The following full account is necessary because *Berthella martensi* has not been rediscovered since it was first described on the basis of three, apparently juvenile specimens over a century ago. Then it was called *Pleurobranchus scutatus* Martens in Möbius, 1880, but that taxon was preoccupied by *Pleurobranchus scutatus* Forbes, 1844, and so the specific name was changed to *martensi* (PILSBRY, 1896). VAYSSIÈRE (1898) re-examined the original specimens.

Berthella martensi can attain 73 mm in extended crawling length, although 30 to 60 mm is usually for mature adults. The body is elongate-oval, smooth, and flat on top. The oral veil and rhinophores are visible anteriorly, but the tail is usually covered by the large, overhanging mantle when the animal is crawling actively; the gill is never visible. The foot is long and parallel-sided, and the tail is almost pointed. There is a large and conspicuous, semi-circular mucus groove anteriorly, and this extends to the squarish, anterior foot corners that are visible in front of the mantle in actively crawling animals.

The mantle is soft (almost gelatinous), smooth or slightly wrinkled (but never pustulose or papillate), very wide with thin margins, and nearly circular. Anteriorly it bears a deep cleft that extends rearwards about one-seventh of the mantle's full length. This cleft reveals the point of fusion of the rhinophores. The mantle's margins are parallel and the posterior edge is broadly rounded. The mantle consists of three large, readily autotomized (see Remarks section) lobes that are fused but distinguishable on the surface by "preformed shear zones," i.e., distinct, narrow, slightly impressed, radial lines at the zones of contact. There are two symmetrical antero-lateral lobes that meet in the midline just behind the rhinophores, and a single posterior lobe. Each antero-lateral lobe meets the posterior lobe postero-dorsally about one-third of the distance from the tail to the head. Mid-dorsally between the three lobes is a smaller, triangular (or "bell-shaped") section that is never autotomized.

The oral veil is trapezoidal and relatively short; its anterior margin is simple and straight. Active specimens sometimes show a weak mid-anterior embayment, but the

margin is never sinuous. Both the upper and lower surfaces of the oral veil are smooth.

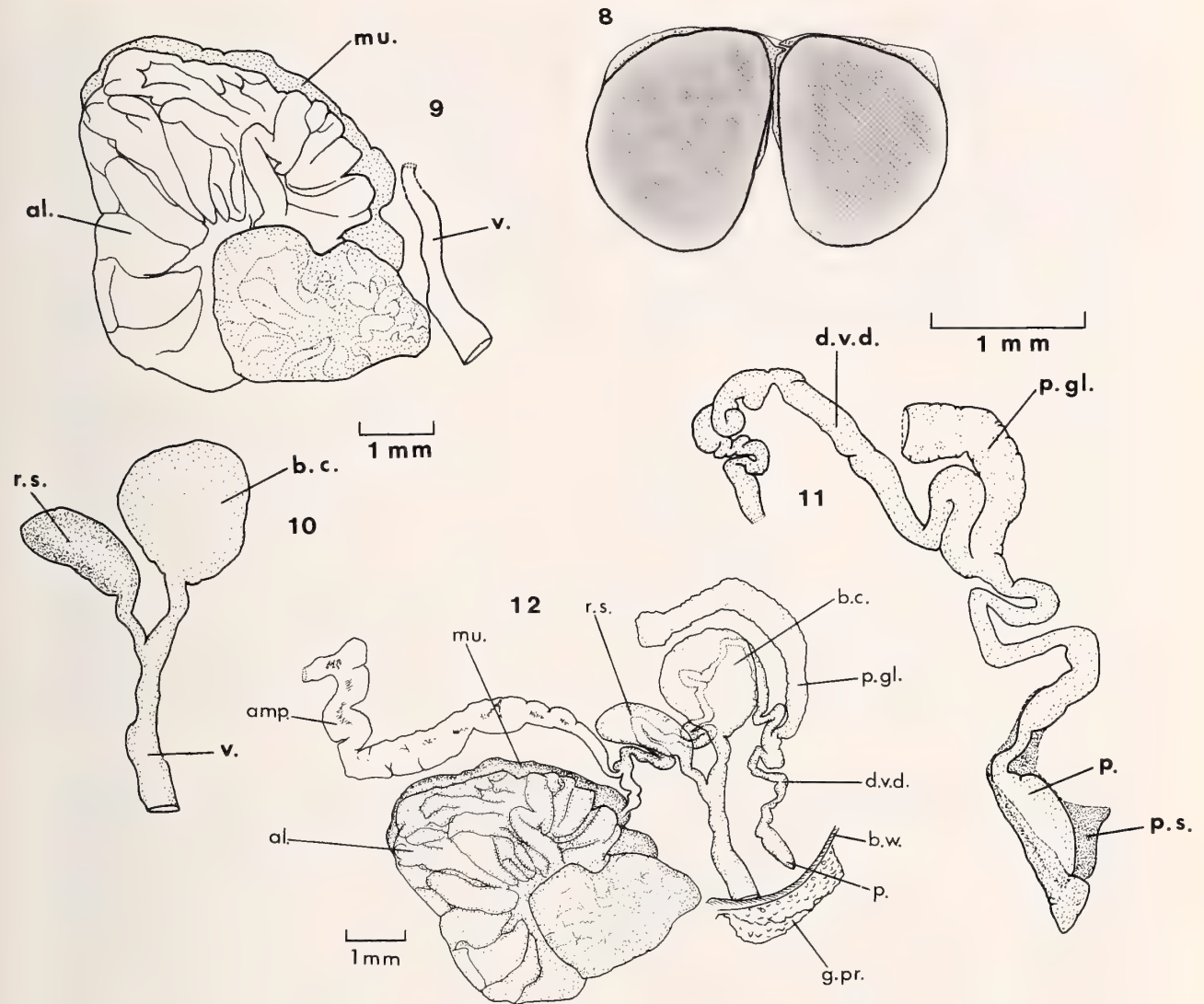
The rhinophores are moderately tall. They arise from a common base which is visible anteriorly when *B. martensi* is crawling. The tips of the rhinophores do not "pulse" in life like those of some *Pleurobranchus* species.

The gill has a smooth rachis and a mean of 16.25 (range 13–19; N = 4) pinnae on the upper side. The anus opens at the hind end of the gill's suspensory membrane.

Coloration is variable (Figures 21 to 25), but now that I have seen 14 specimens I believe the limits of variation can be ascertained and described. The upper body and mantle have a ground color of pale ochre, pale reddish-brown, light brown, amber, or yellowish- or creamish-brown, and there is an overlay of few or many irregular, chocolate or dark purplish-brown spots. These spots are usually small and evenly spaced (Figures 21, 22, and 24), but there can also be only a few large ones (Figure 25; KUITER, 1982) or none at all (Figure 23). With magnification, the brown spots resolve into dense aggregations of purple-brown flecks. The margins of the central triangle on the mantle usually have a chocolate line, and there is always a longitudinal streak of the same color mid-dorsally on the tail (Figures 23 and 25). The shear zones on the mantle are sometimes indicated by brown lines. Other parts of the body that have wide or narrow brown lines are the antero-lateral corners and anterior margin of the oral veil, the rhinophores (but not the common rhinophoral base), the anterior mucus groove, the foot, and the gill rachis. A thin brown line extends continuously all round the body at the junction of the foot and mantle. A second line, which is stronger and darker, extends on the right side backwards from the corner of the oral veil to the start of the gill; in doing so it passes above the genital apertures. On the left side an identical line extends about one-third of the way along the body. These two lateral lines and the mid-dorsal, longitudinal tail streak are the markings that are most consistent on all specimens. The brown pigment is easily rubbed off, even in living specimens. The body tissues are quite translucent; for example, the brown gill rachis is visible through the side of the mantle when the mantle is pressed against the body. The shell and viscera are usually faintly visible beneath the mantle. The foot sole is usually milky-white or pale amber in contrast to the mantle and upper body.

Berthella martensi is a lethargic pleurobranch. It is highly photonegative and hides during the day beneath ledges and boulders. Mr. Johnson informs me that in Hawaii he has observed 18 specimens that were actively crawling at night. The mantle can produce a white fluid when *B. martensi* is disturbed. The mantle lobes are autotomized very readily by rough handling or preservation (see Remarks section for further discussion).

The shell (Figures 30 to 32) that lies beneath the triangular area in the center of the mantle is small, about one-third of the adult body length. The shell's protoconch



Explanation of Figures 8 to 12

Jaws and reproductive system of *Berthella martensi*. Figure 8. Both jaws separated and laid flat showing inner surface. Figure 9. Detail of nidamental glands. Figure 10. Detail of seminal receptacles. Figure 11. Detail of structures associated with distal section of vas deferens and penis; penial sheath cut longitudinally. Figure 12. Composite view of structure of reproductive organs of a mature individual (penial sheath removed). Abbreviations used in Figures 9 to 12: al., albumen gland; amp., ampullar region of hermaphrodite duct; b.c., bursa copulatrix; b.w., cut body wall; d.v.d., distal section of vas deferens; g.pr., genital protuberance; mu., mucus gland; p., penis; p.gl., penial gland; p.s., penial sheath; r.s., receptaculum seminis; v., vagina.

lies beneath the rear of the central area, and its abapical margin does not quite extend to the front of the central area. Thus, the shell covers the anterior section of the digestive gland, ovotestis, and pericardium. It is slender, elongate, and calcified. The apex is narrow and the protoconch elevated; the posterior rim is always lower than the protoconch, and the outer lip slopes sharply away posteriorly without any flare (Figures 31 and 32). The right and left margins are nearly parallel. The abapical

margin is evenly rounded, and not truncated. The abapical section is evenly convex, not flattened as in *Berthellina citrina*. The columellar slope on the left side (when the shell is dorsal) is almost flat, not steep. The only sculpture consists of undulating, concentric ridges (Figure 30). The shell is glossy because of an entire periostracal layer; the periostracum does not extend beyond the margins. The shell is amber. The shell drawn by VAYSSIÈRE (1898:pl. 18, fig. 45), which was 6 mm long by 3 mm wide, matches

Explanation of Figures 13 to 20

Figure 13. *Pleurehdera haraldi*; length 40 mm. From 3 m, Enewetak Island, Enewetak Atoll, 19 Sept. 1981. Photograph: S. Johnson.

Figure 14. *Pleurehdera haraldi*; length 22 mm. From 2 m, Lujor Island channel, Enewetak Atoll, Sept. 1981. Photograph: S. Johnson.

Figure 15. *Pleurehdera haraldi*; length 28 mm. From 3 m, Enewetak Island, Enewetak Atoll, Sept. 1981. Photograph: S. Johnson.

Figure 16. *Pleurehdera haraldi*; length 22 mm. From 12 m, Puapukea, Oahu Island, Hawaii, August 1980. Photograph: S. Johnson.

Figure 17. *Berthella pellucida*; length 14 mm. From 8 m, Bokandretok/Madren Reef, Enewetak Atoll, 19 Nov. 1982. Photograph: S. Johnson.

Figure 18. *Berthella pellucida*; length 22 mm. From 0 m, Myora, Moreton Bay, southern Queensland, 21 Sept. 1981. Photograph: R. C. Willan.

Figure 19. Photomicrograph of mandibular elements of *Pleurehdera haraldi*; from inner face of jaw. Specimen from 3 m, Enewetak Atoll, 23 Nov. 1981. Bar = 40 μ m.

Figure 20. Photomicrograph of mandibular elements of *Pleurehdera haraldi*; from inner face of same jaw as Figure 19. Bar = 40 μ m.

Explanation of Figures 21 to 28

Figure 21. *Berthella martensi*; length 28 mm. From 2 m, Jinimi Island, Enewetak Atoll, Sept. 1981. Photograph: S. Johnson.

Figure 22. *Berthella martensi*; length 23 mm. From 4 m, Enewetak Island, Enewetak Atoll, Sept. 1981. Photograph: S. Johnson.

Figure 23. *Berthella martensi*; length 36 mm. From 8 m, Puako, Hawaii Island, Hawaii, Aug. 1980. Photograph: S. Johnson.

Figure 24. *Berthella martensi*; length 39 mm. From 8 m, N.W. of Point Lookout, North Stradbroke Island, southern Queensland, 25 March 1983. Photograph: R. C. Willan.

Figure 25. *Berthella martensi*; length 73 mm. From 8 m, N.W. coast of Lizard Island, northern Queensland, 9 Oct. 1982. Photograph: R. C. Willan.

Figure 26. Enlarged reproduction of VAYSSIÈRE's (1898, pl. 18, fig. 44) illustration of a paratype of *Pleurobranchus scutatus* Martens in Möbius, 1880; length of actual preserved specimen 13.5 mm.

Figure 27. Photomicrograph of mandibular elements of *Berthella martensi*, showing typical elements from inner face of jaw. Specimen from 10 m, Jedrol Island, Enewetak Atoll. Bar = 50 μ m.

Figure 28. Photomicrograph of mandibular elements of *Berthella martensi*; from inner face of jaw. Specimen from 10 m, No Bull Pinnacle Number 2, Enewetak Atoll. Area depicted is near dorsal margin showing weak denticles flanking main cusp. Bar = 50 μ m.

Explanation of Figures 29 to 36

Figure 29. External (right) and internal (left) views of shell of *Berthella pellucida*; length 6.4 mm \times width 4.1 mm. Specimen from 18 m, Bokandretok/Madren reef, Enewetak Atoll, 19 Nov. 1982; extended crawling length 14 mm.

Figure 30. External (right) and internal (left) views of shell of *Berthella martensi*; length 11.2 mm \times width 4.7 mm. Specimen from 10 m, Puako, Hawaii, 24 Oct. 1980; preserved length 24 mm.

Figure 31. External (right) and internal (left) views of shell of juvenile *Berthella martensi*; length 5.5 mm \times width 3.0 mm. Specimen from 10 m, No Bull Pinnacle Number 2, Enewetak Atoll, 30 May 1982; extended crawling length 12 mm.

Figure 32. External (right) and internal (left) views of shell of

Berthella martensi; length 10.6 mm \times width 4.7 mm. Specimen from 10 m, Jedrol Island, Enewetak Atoll, 23 April 1982; extended crawling length 25 mm.

Figure 33. SEM of middle lateral teeth from radula of *Berthellina citrina*. Specimen from 1 m, Bokandretok Reef, Enewetak Island, 22 May 1982. Bar = 40 μ m.

Figure 34. SEM of inner lateral teeth from same radula of *Berthellina citrina* as shown in Figure 33. Bar = 20 μ m.

Figure 35. SEM of entire right jaw laid flat showing inner surface. Bar = 1 mm.

Figure 36. SEM showing detail of mandibular elements from inner surface of same jaw as shown in Figure 35. Bar = 40 μ m.

Explanation of Figures 37 to 44

Figure 37. SEM of midline (right) and inner lateral teeth from radula of *Berthella pellucida*. Specimen from 2 m, Enewetak Island, 19 Sept. 1982. Bar = 20 μ m.

Figure 38. SEM of middle lateral teeth from same radula of *Berthella pellucida* as shown in Figure 37. Bar = 20 μ m.

Figure 39. SEM of outer lateral teeth close to edge of same radula of *Berthella pellucida* as shown in Figure 37. Bar = 20 μ m.

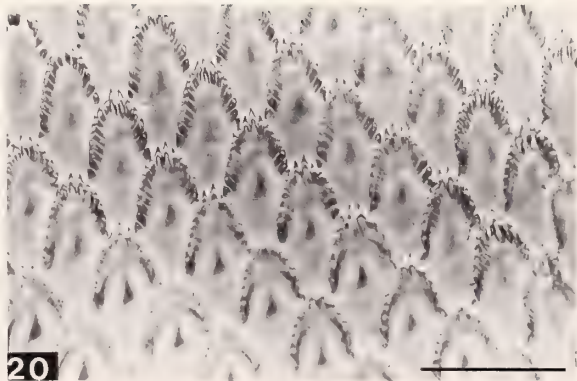
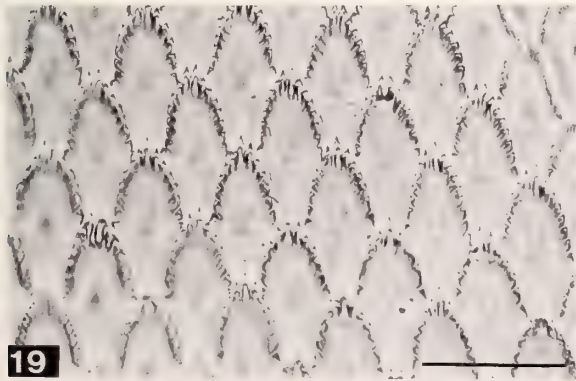
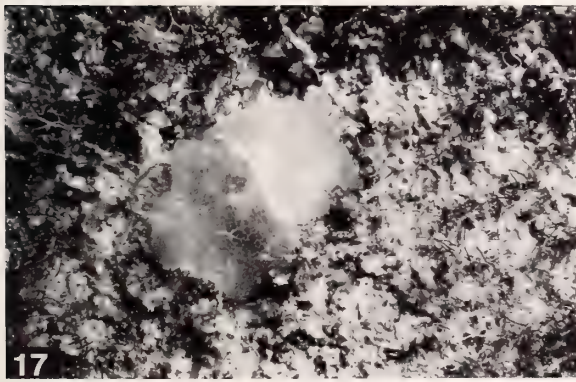
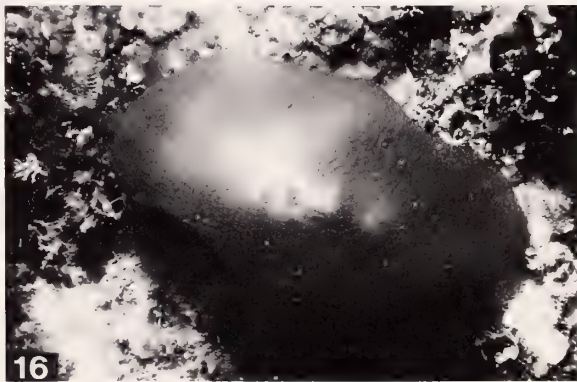
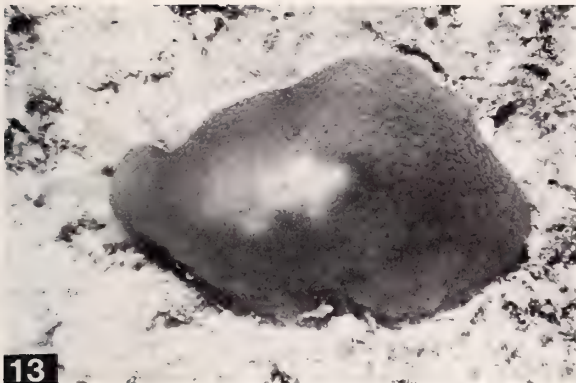
Figure 40. SEM of middle lateral teeth from radula of *Berthella martensi*. Specimen from 10 m, Puako, Hawaii, 24 Oct. 1980. Bar = 20 μ m.

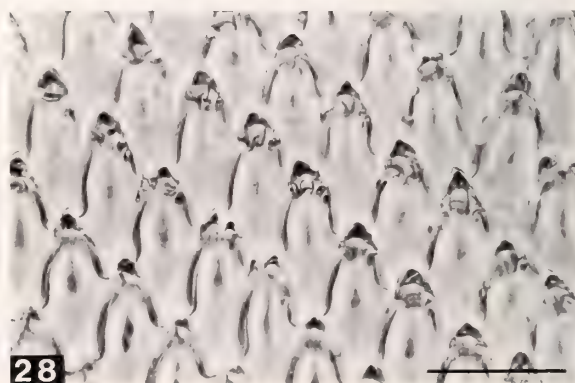
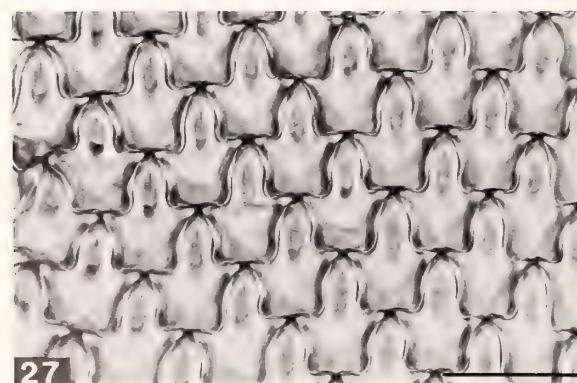
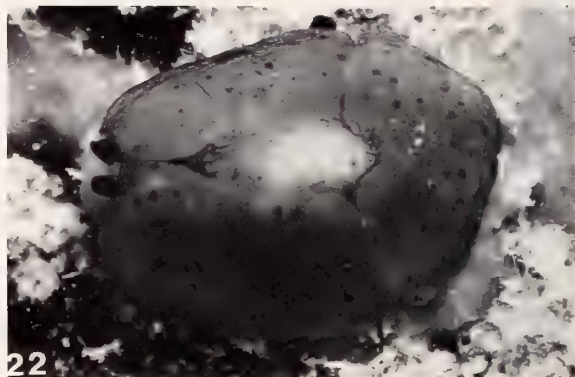
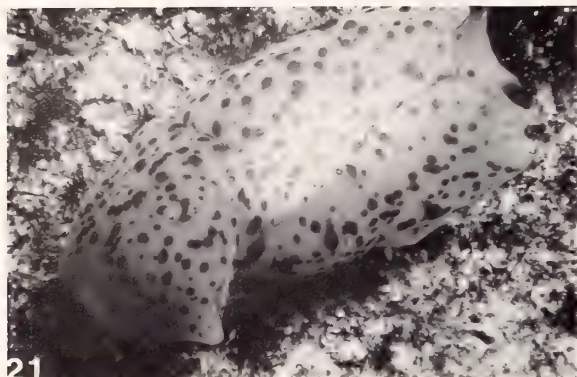
Figure 41. SEM showing detail of middle lateral teeth from same radula of *Berthella martensi* as shown in Figure 40. Bar = 20 μ m.

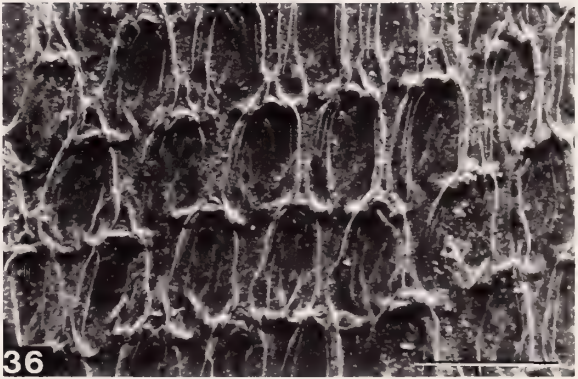
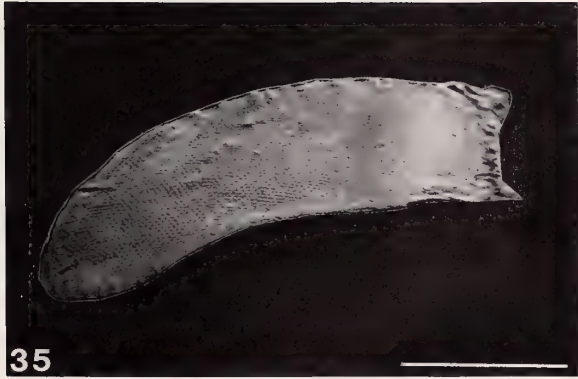
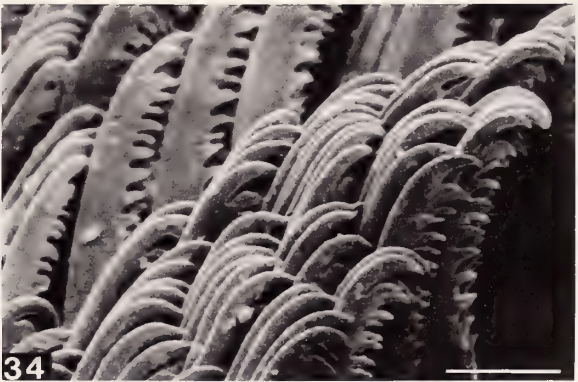
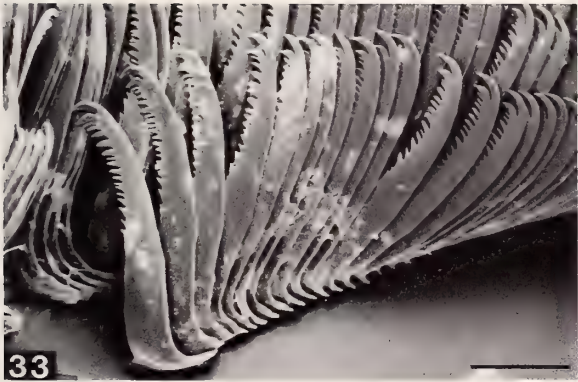
Figure 42. SEM of outermost lateral teeth from same radula of *Berthella martensi* as shown in Figure 40. Bar = 20 μ m.

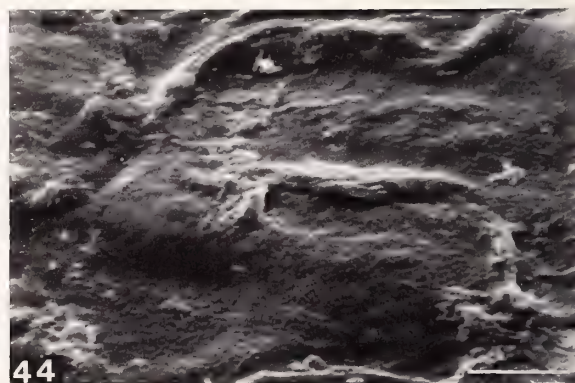
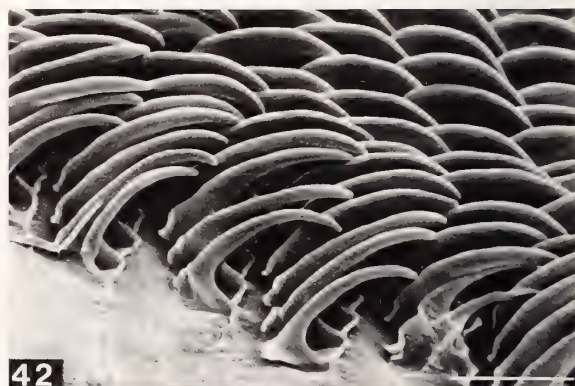
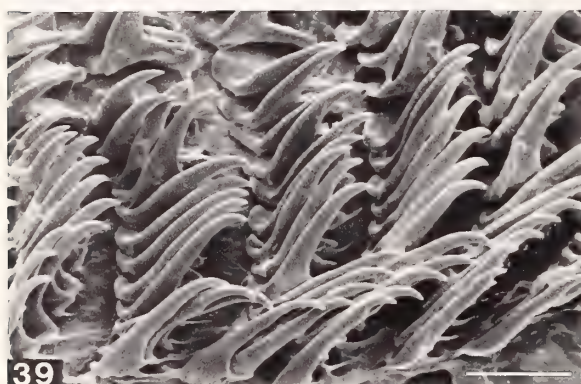
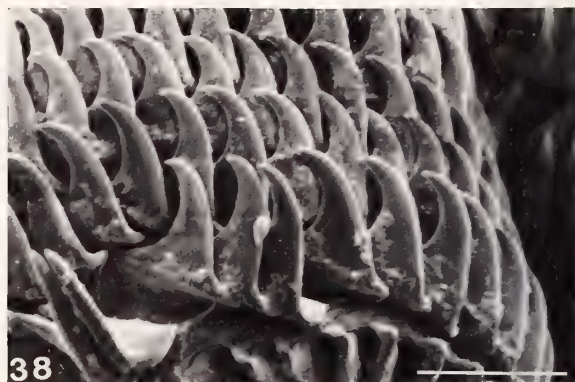
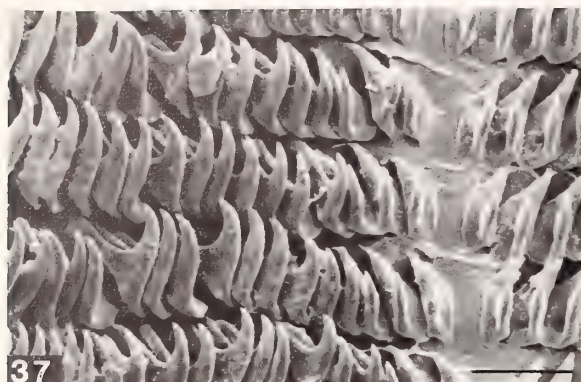
Figure 43. SEM showing detail of mandibular elements from inner surface of jaw of same *Berthella martensi* as shown in Figure 40. Bar = 40 μ m.

Figure 44. SEM showing high magnification of mandibular element from inner surface of jaw of *Berthella pellucida*. Specimen from 2 m, Enewetak Island, 19 Sept. 1982. Note shagreened texture. Bar = 4 μ m.









closely that of the smaller No Bull Pinnacle specimen (Figure 31).

Radulae from three Marshall Islands, two Australian and one Hawaiian specimen were stained and mounted on slides; the radula of the second Hawaiian specimen was coated and mounted on a stub for SEM study. One Hawaiian specimen was 24 mm long preserved; its radula measured 3.0 mm long by 3.0 mm wide when flattened on a slide; and its radular formula was $104 \times 186.0.186$ (sizes of teeth given below relate to this radula). The radular formula for the second Hawaiian specimen, which was a similar length, was $93 \times 158.0.158$. The larger No Bull Pinnacle specimen was 16 mm long preserved; its radula measured 2.0 by 2.8 mm; and its radular formula was $82 \times 124.0.124$. The smaller No Bull Pinnacle specimen was 8 mm long preserved; its radula measured 1.9 by 1.3 mm; and its radular formula was $57 \times 92.0.92$. The Enewetak Island specimen was 15.5 mm long preserved; its radula measured 2.0 by 1.5 mm; and its radular formula was $66 \times 84.0.84$. A general formula for adult *B. martensi* is $82-104 \times 124-186.0.124-186$.

The buccal mass is particularly large and consists of two jaws with a small radular sac postero-ventrally between them. The floor of the buccal mass between the jaws is slightly concave. The innermost lateral teeth (Figure 40) have relatively narrow blades, much-recurved cusps, and elongate basal plates; they measure 16 μm in vertical height, and their basal plates measure 22 μm in length. The middle laterals (Figure 41) are somewhat larger (24–30 μm in vertical height) and equally curved. The outermost laterals (Figure 42) have tall, narrow, curved (not erect or peg-like) blades; they measure about 30 μm in vertical height.

The jaws (Figure 8) are particularly large and nearly round; the ventral margin is straight, the anterior margin is subtruncate, and the dorsal and posterior margins are convex and evenly rounded. The height (2.9 mm for a Hawaiian specimen) is a little greater than the width of a single jaw (2.5 mm). The mandibular elements constituting the jaws are cruciform with narrow blades, conspicuous lateral projections, and broad bases. The elements of all seven sets of jaws I examined were smooth (Figure 27), except for some elements eight to ten rows in from the dorsal margin of the larger No Bull Pinnacle specimen, which had one to three, irregular denticles flanking the cusp (Figure 28). The Hawaiian specimen examined with the SEM (Figure 43) had thickened margins, and both the No Bull Pinnacle specimens had elongate, thickened apices to their blades. The height of the elements from the Hawaiian specimen whose jaw dimensions are given above is 75–80 μm ; the width between projections is 60–62 μm ; and the width across the base of an element is 40–45 μm .

Reproductive systems were dissected from the Jedrol Island specimen (the other Marshall Islands specimens were badly preserved), the two Hawaiian specimens, and the two Queensland specimens. The reproductive system

is typical of the genus *Berthella* and is shown in Figures 9 to 12. Significant details are as follows. A genital papilla is present on the preserved specimens; it is a relatively large, flat-topped mound; and it bears small pustules over its surface. The penis is relatively small, simple, and conical. The penial gland arises far back on the vas deferens. The vas deferens is not expanded into a prostate gland. The receptaculum seminis arises high up the vagina (approximately two-thirds of the distance to the bursa copulatrix).

Berthella martensi lays a flaccid, white spawn coil. Ova measuring 75–95 μm occur singly in capsules (up to 190 μm diameter) that are loosely coiled in cylinders within the spawn. Approximately 315 ova make up a single coil. Two egg masses laid in the laboratory by a 40 mm Enewetak Island specimen on the same day contained about 55,000 and 40,000 ova respectively (L. Boucher, personal communication, 1983).

Abundance

Mr. Johnson recorded 17 specimens of *Berthella martensi* between July 1981 and February 1983. All were found beneath dead coral at depths ranging from 2 to 12 m. The species occurs in clean-water habitats, being found in both lagoonal situations and on inter-island reefs. Mr. Johnson has observed the different color forms tending to pair with their own color form; of four copulating pairs seen, only one was mixed.

Remarks

One of the most characteristic behaviors of *Berthella martensi* is that of mantle autotomy. The mantle breaks along any two of the "preformed shear zones" and any of the three lobes can be autotomized. The central triangular area is never shed. Of the three type specimens, one had evidently autotomized the anterior left lobe and another had autotomized the anterior right lobe. My specimen from Lizard Island, Queensland, had autotomized the posterior lobe, and this had evidently regrown but not fused with the anterior lobes, nor had the dark spots been reproduced. Among the Marshall Islands material, the larger No Bull Pinnacle specimen and the Jedrol Island specimen had autotomized both the anterior lobes; the Enewetak Island specimen and smaller No Bull Pinnacle specimen both had split their mantles along the three "shear" zones, but none of the lobes had been fully autotomized. One of the Hawaiian specimens had autotomized the posterior lobe and the other both the anterior lobes. On being narcotized, my specimen from southern Queensland autotomized its anterior right lobe, and then it resembled perfectly VAYSSIÈRE's diagram (1898:pl. 18, fig. 44), reproduced here in Figure 26.

Since *Berthella martensi* never autotomizes the central triangular area, its shell is never exposed. Therefore, VAYSSIÈRE (1898) was perfectly correct in not admitting

Pleurobranchus scutatus into Pilsbry's genus *Gymnotoplax* (type species *Pleurobranchus americanus* Verrill, 1885) in which the shell was supposedly exposed in the living animal. In fact, as WILLAN (1978) has shown, that assumption by Pilsbry was also incorrect, and no member of the Pleurobranchidae exists in the living state with a shell that is wholly or partially uncovered.

The only other pleurobranch known to autotomize its mantle is the similar-looking *Berthella kaniae* Sphon, 1972, that ranges from west Mexico to Panama in the tropical, eastern Pacific Ocean. That species autotomizes irregular chunks of its mantle border (SPHON, 1972) and apparently has no "preformed shear zones" on the mantle; neither does it have a deep cleft anteriorly.

Besides mantle autotomy, other unique features of *Berthella martensi* are the deep anterior cleft in the mantle, the spotted mantle, the tail streak, the lines along the body, the elongate and convex shell, the high radular formula, the small teeth, the curved (not erect) outer lateral teeth, the large rounded jaws, and branching off of the penial gland far back along the distal vas deferens. The features in which the central Pacific specimens match the original Indian Ocean specimens of *Berthella martensi* are mantle autotomy, the anterior cleft, the spotted mantle, the shell and jaw shapes, the radular tooth shape, the large jaws, and the wide-based mandibular elements. The only significant difference between the two is the denticulate mandibular elements in the former, but as I have shown earlier in this paper, these elements show great intraspecific variation in pleurobranchs.

ACKNOWLEDGMENTS

I am particularly grateful to Mr. Scott Johnson for sending me this collection of pleurobranchs together with slides and information about the living animals. Ms. Lisa Boucher kindly supplied the data on the spawn of *Berthella martensi*. Mr. Johnson also sent additional material from Hawaii. Comparative photographs were generously made available by Mr. R. Burn, Mr. N. Coleman, and Dr. P. Morse. Mr. Johnson, Mr. Burn, and Dr. E. Marcus read and offered criticisms of the manuscript.

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A New Species of *Gastropteron* from Florida (Gastropoda: Opisthobranchia)

by

TERRENCE M. GOSLINER¹

Division of Mollusks, National Museum of Natural History,
Smithsonian Institution, Washington, D.C. 20560

AND

PATRICIA T. ARMES

410 N.W. 134th Way, Plantation,
Florida 33325

Abstract. The morphology and biology of *Gastropteron vespertilium* Gosliner & Armes, spec. nov., from Tampa Bay, Florida, are described. A detailed comparison of *G. vespertilium* with *G. rubrum* (Rafinesque, 1814) is provided, and consistent differences are noted.

INTRODUCTION

MEMBERS OF the Gastropteridae are widely distributed throughout the world's oceans. Only 3 of the 20 described species have been recorded from the Atlantic Ocean (Gosliner, in press), with only a single species known to occur in the western Atlantic (MARCUS, 1977).

In April, 1970, one of us (PTA) discovered a population of an undescribed species of *Gastropteron* from intertidal mudflats in Tampa Bay, Florida. Repeated observations have been made in successive years. This paper describes aspects of the morphology and biology of this species and discusses its systematic placement.

All figures, unless otherwise indicated were prepared by one of us (TMG).

DESCRIPTION

Gastropteron vespertilium
Gosliner & Armes, spec. nov.

Type material: (1) Holotype: National Museum of Natural History, Washington, D.C., USNM 809992, 1 specimen, swimming at surface, Bunces Pass, Tampa Bay, Pinellas County, Florida, 1 February 1970, collected by C. Powell. (2) Paratype: USNM 809993, one dissected specimen with radular slide, Bunces Pass, Tampa Bay,

Florida, 1 February 1970, C. Powell. (3) Paratype: USNM 809994, one dissected specimen, slides of radula, penis and reproductive organs, Bunces Pass, Tampa Bay, Florida, 1 February 1970, C. Powell.

Etymology: The specific epithet is derived from the Latin *vespertilio*, meaning "bat." When it is swimming by flapping its parapodia, *Gastropteron vespertilium* resembles a bat.

Distribution: Specimens have been found at only four localities (Figure 1): Boca Ciega Inlet, Capri Island, the north end of the Skyway Bridge, and Bunces Pass, all within the vicinity of Tampa Bay, Florida.

External morphology: The living animals (Figures 2 to 5) are 3-5 mm in length and may reach 8 mm in width when the parapodia are fully opened. The ground color of the head, parapodia, and foot of the living animals varies from charcoal-gray to purplish black. A line of brilliant yellow is generally present around the margins of the parapodia and siphon. In some specimens the margin is greenish or pale blue, with scattered blue-gray spots on the parapodia. The flagellar appendage is charcoal-gray basally and translucent white with occasional spots of gray in its apical half. The head shield is triangular, slightly emarginate antero-medially. Its posterior end is folded to form a simple tubular siphon. The parapodia are thin and fleshy. The foot (Figure 7) is broad and extends posteriorly behind the parapodia. Its posterior limit is trian-

¹ Permanent address: Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, CA 94118.

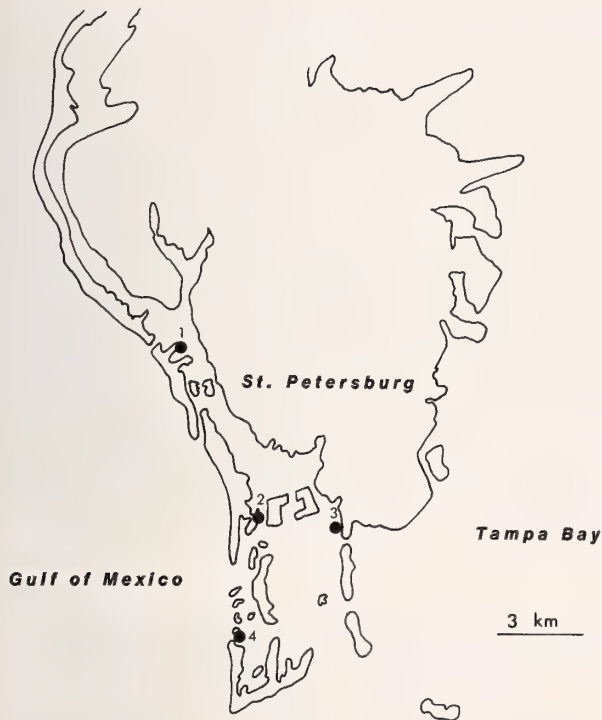


Figure 1

Collecting localities of *Gastropterion vespertilium* spec. nov.: 1, Capri Island; 2, Boca Ciega Inlet; 3, north end of Sunshine Skyway Bridge; 4, Bunces Pass.

gular and acute. Anteriorly, the foot is emarginate. A pedal gland empties by means of an elongate groove at the posterior limit of the foot.

The gill (Figure 8) is situated on the right side of the body and consists of 9 to 11 simply plicate leaflets. The anus is situated immediately posterior to the gill. The hermaphroditic gonopore is anterior to the gill and empties into the sperm groove, which transports endogenous sperm to the male gonopore on the right side of the head. The flagellum (Figures 2, 3, and 8) is situated on the right side of the body and when fully extended may equal half of the body length. Frequently the flagellum is partially or completely retracted and may be entirely enveloped by the parapodia.

Shell: The weakly calcified, hyaline shell (Figures 6 and 23A) is 350 μm in length and consists of approximately two complete whorls.

Digestive system: The buccal mass is elongate and highly muscular. The radula sac is situated at the posterior limit of the buccal mass. In the anterior portion of the mass is a thin labial cuticle which possesses several rows of minute polygonal platelets (Figure 9). The radula (Figures 10 to 15) is well developed with a formula of $15-21 \times 5-6.1.0.1.5-6$. The inner lateral teeth possess 17-25 minute

denticles. The outer lateral teeth lack denticles and gradually decrease in size toward the outer margin of the radula.

Central nervous system: All of the ganglia are contained within a circum-esophageal nerve ring (Figure 16). The cerebral ganglia are separated by a short commissure. Anteriorly, each cerebral ganglion gives rise to an enlarged area and subsequently bifurcates into two nerves. The pedal ganglia are joined by a commissure that is slightly more elongate than the cerebral commissure. Adjacent to the left cerebral ganglion is the left pleural ganglion, which is also joined to the left pedal ganglion. The subintestinal and visceral ganglia are adjacent to the left pleural ganglion. From the visceral ganglion the visceral loop passes ventral to the esophagus and curves anteriorly to the suprainestinal ganglion on the right side of the nerve ring. The suprainestinal ganglion is adjacent to the right pleural ganglion.

Reproductive system: The ovotestis is situated at the posterior end of the visceral hump. From there a narrow convoluted ampulla (Figure 17) is directed anteriorly. It winds around the female gland mass and joins the duct of the bursa copulatrix and the female gland mass at the hermaphroditic gonopore. The ampulla lacks a distinct receptaculum seminis in the two specimens examined. The albumen and membrane glands are small and difficult to discern, while the mucous gland comprises the bulk of the female gland mass. The bursa copulatrix is spherical. The penis (Figure 18) consists of an elongate prostate which is thick and sharply curved. On the inner side of the posterior end of the prostate is a spherical spermatid bulb that joins the prostate by means of an elongate duct. The penial papilla is short and rounded with a bilobed apex.

NATURAL HISTORY AND BEHAVIOR

Gastropterion vespertilium has been found only in the vicinity of Tampa Bay. The three specimens that comprise the type series were collected in early February, but the numerous specimens collected at Boca Ciega Bay were all found in April in several successive years. During April the animals were abundant and occurred with egg masses. By early May the population had entirely disappeared. It is likely that the animals come into shallow water to breed. This also is true for the nudibranch *Dendronotus iris* along the California coast (TMG, personal observation), which normally inhabits subtidal flats but is found commonly in the intertidal during summer months when it is breeding. It is interesting to note that both of these opisthobranchs have remarkable natatory capabilities which facilitate their transport.

Gastropterion vespertilium is found on intertidal sand flats amid scattered plants of shoal grass, *Diplanthera wrightii* Escher. The animals commonly crawl along the surface of the substratum and occasionally burrow, but like most known members of the Gastropteridae, they are



Explanation of Figures 2 to 5

Gasteropteron vespertilium spec. nov. Figure 2. Lateral view (photograph by Rod Armes). Figure 3. Dorsal view (photograph by Patricia Armes). Figure 4. Animal depositing egg mass (photograph by Patricia Armes). Figure 5. Animal swimming (photograph by Rod Armes).

also capable of swimming for prolonged periods (Figure 5). The animals swim by dorsal-ventral flapping of the parapodia. The body is sometimes upright, but more frequently inverted while swimming. Swimming is erratic, characterized by rapid circling and darting. While swimming, the animals often protrude the buccal region and a white, viscous fluid is secreted. Little is known about feed-

ing in the Gasteropteridae, but the remains of minute crustaceans were found in the stomach of several specimens of *G. vespertilium*.

Extensive laboratory and field observations were made of individuals undergoing copulation and egg deposition. Copulation lasted 5-10 min in the pairs observed. The egg mass (Figure 4) emerges from the hermaphroditic

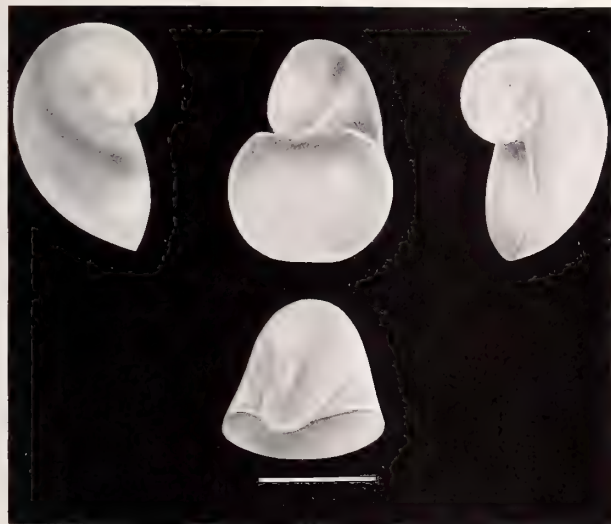


Figure 6

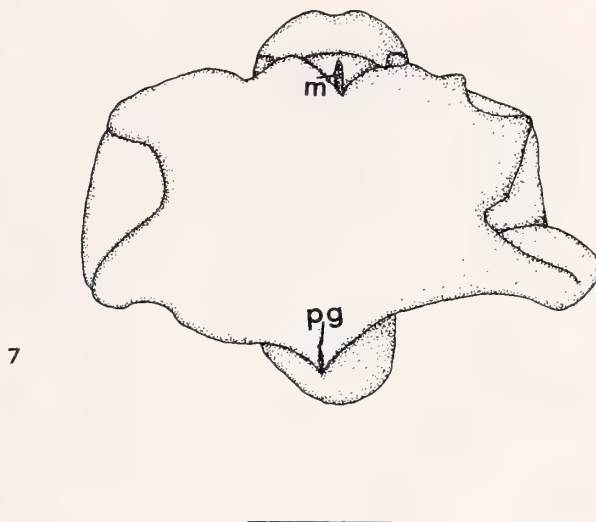
Shell of *Gastropteron vespertilium* spec. nov. Scale = 175 μ m (drawing by Sally D. Kaicher).

gonopore as a single strand of eggs enveloped by a coating of mucus. There is generally a single yellowish egg per capsule. Sixteen to twenty capsules are emitted at a rate of one per second, followed by a three to four second pause before another strand emerges. This procedure may continue for 20 min to an hour. The strands are formed into a spherical mass, which is variable in size. Veliger larvae hatched within three or four days of egg deposition.

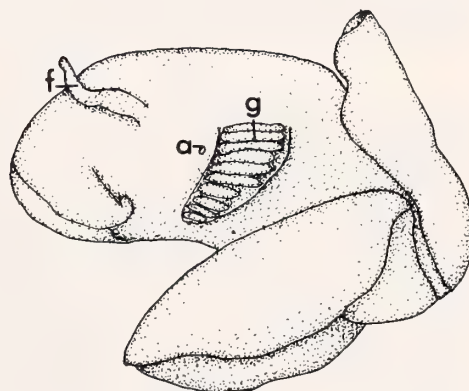
When touched and seriously disturbed, specimens of *Gastropteron vespertilium* exude a bright greenish-yellow fluid that leaves a persistent yellow-orange stain that is soluble in alcohol but not in water. While trying to relax animals for fixation, it was determined that they could withstand temperatures as low as 0°C for 15 min and still revive. They died when the temperature was lowered to -1°C for the same period.

DISCUSSION

The species of Gastropteridae are readily distinguishable on the basis of the external morphology and coloration of the living animal. *Gastropteron vespertilium* can be differentiated from all other described members of the family by its dark-gray or blue-black color. *Gastropteron vespertilium* is placed in *Gastropteron* by virtue of its radula, which contains five or six outer lateral teeth per half row. Of the 14 previously described species of *Gastropteron* only four, *G. citrinum* Carlson & Hoff, 1974, *G. fuscum* Baba & Tokioka, 1965, *G. ladrones* Carlson & Hoff, 1974, and *G. rubrum* (Rafinesque, 1814), possess a single elongate flagellum on the right side of the body, as in *G. vespertilium*. The first three species possess a vestigial gill and only *G. vespertilium* and *G. rubrum* have an elongate flagellum and a well-developed gill. *Gastrop-*



7



8

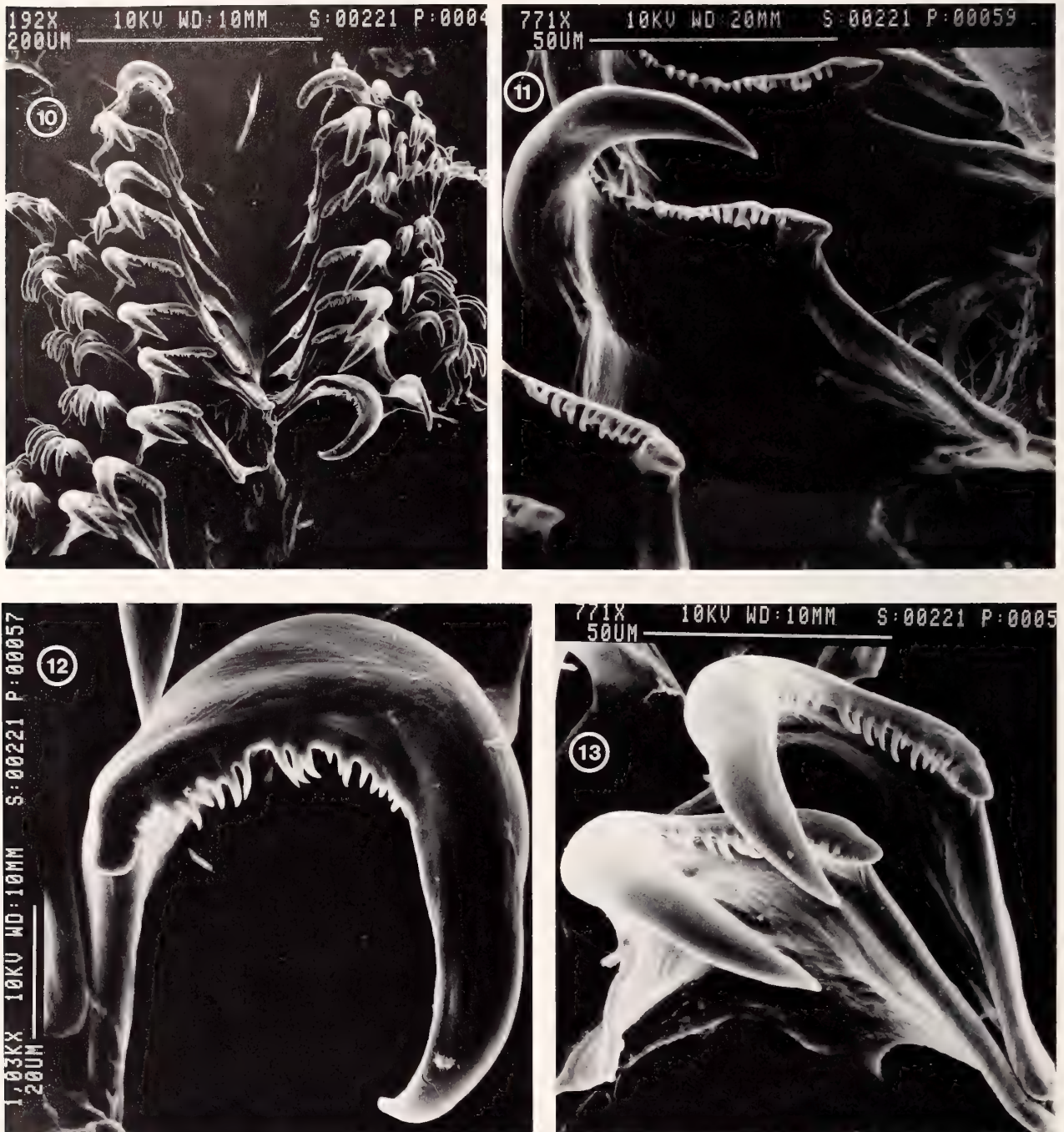
Explanation of Figures 7 and 8

Gastropteron vespertilium spec. nov. Scale = 1.0 mm. Figure 7. Ventral view: m, mouth; pg, pedal gland. Figure 8. Right lateral view: a, anus; f, flagellum; g, gill.



Figure 9

Jaw of *Gastropteron vespertilium* spec. nov. Scale = 0.25 mm.



Explanation of Figures 10 to 13

Gastropteron vespertilium spec. nov. Scanning electron micrographs of radular teeth. Figure 10. Entire radular width. Figures 11 to 13. Inner lateral teeth from various angles.

teron rubrum is also the only other species of the family known from the western Atlantic (MARCUS, 1977). For these reasons a detailed comparison of *G. rubrum* and *G. vespertilium* is provided. In addition to records of *G.*

rubrum from the literature (VAYSSIÈRE, 1880, 1885; BERGH, 1893; GUIART, 1901; MARCUS & MARCUS, 1966; SALVINI-PLAWEN & ABBOTT, 1974), specimens from Palermo, Italy (four specimens, Museum National d'His-

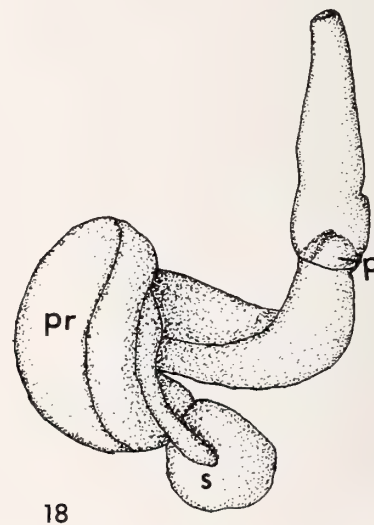
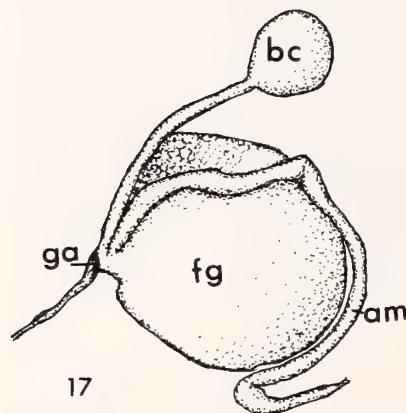
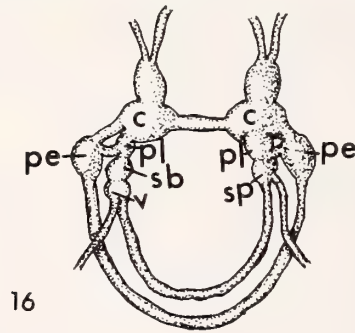


Explanation of Figures 14 and 15

Gastropteron vespertilium spec. nov. Scanning electron micrographs of radular teeth. Figure 14. Half rows of teeth. Figure 15. Outer lateral teeth.

Table 1
Morphological comparison of *Gastropteron rubrum* and *G. vespertilium*.

	Reference, locality	# of gill lamellae	Radular formula	# denticles on inner lateral	Prostate	Spermatic bulb
<i>Gastropteron rubrum</i>	VAYSSIÈRE, 1880, 1885 Mediterranean	—	40X5.1.0.1.5.	26	elongate	absent
<i>Gastropteron rubrum</i>	BERGH, 1893 Naples	25–30	20–23X5.10.1.5.	4–18	elongate	absent
<i>Gastropteron rubrum</i>	MARCUS, 1960; present study Bear Cut, Key Biscayne	11	17X5–6.1.0.1.5–6.	15–18	elongate	absent
<i>Gastropteron rubrum</i>	present study Grand Cayman Is.	10	20X5–6.1.0.1.5–6.	16–28	elongate	absent
<i>Gastropteron rubrum manx</i>	MARCUS & MARCUS, 1966; present study Gulf of Guinea	23	23X5.1.0.1.5.	18–26	elongate	absent
<i>Gastropteron vespertilium</i>	present study Tampa Bay	9–10	15–27X5.6.1.0.5–6.	17–25 ¹	short	present



Explanation of Figures 16 to 18

Gastropteron vespertilium spec. nov. Scale = 1.0 mm. Figure 16. Central nervous system: c, cerebral ganglion; pe,



Explanation of Figures 19 and 20

Figures 19 and 20. *Gastrophteron rubrum* (Rafinesque, 1814). Radular teeth of specimen from Grand Cayman Island. CASIZ 034121.

pedal ganglion; pl, pleural ganglion; sb, subintestinal ganglion; sp, suprainintestinal ganglion; v, visceral ganglion.
Figure 17. Reproductive system: am, ampulla; bc, bursa copulatrix; fg, female gland mass; ga, genital aperture.
Figure 18. Penis: p, penis; pr, prostate; s, spermatic bulb.



Explanation of Figures 21 and 22

Figures 21 and 22. *Gastropoton rubrum* (Rafinesque, 1814). Radular teeth of specimen from Bear Cut, Key Biscayne. USNM 836667.

toire Naturelle, Paris), Grand Cayman Island (one specimen, California Academy of Sciences, San Francisco, CASIZ 034121, Grand Cayman Island, Seven Mile Beach, Caribbean Club, 150 m off shore, just below surface, col-

lected by James E. Sutton, 30 June 1974) and Miami, Florida (one specimen, National Museum of Natural History, USNM 836667, Bear Cut, Biscayne Bay, collected by Sandra Maxwell, 21 May 1966) were examined.

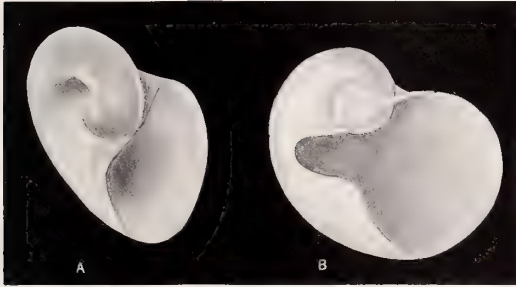


Figure 23

Shells. A. *Gastropteron vespertilium* spec. nov. B. *Gastropteron rubrum* (Rafinesque, 1814), after Vayssi re, 1885. Not to scale (drawing by Sally D. Kaicher).

The holotype of *G. rubrum manx* Marcus & Marcus, 1966 (National Museum of Natural History, Washington, USNM 576262, Gulf of Guinea, R.V. Pillsbury station 241) was also reexamined.

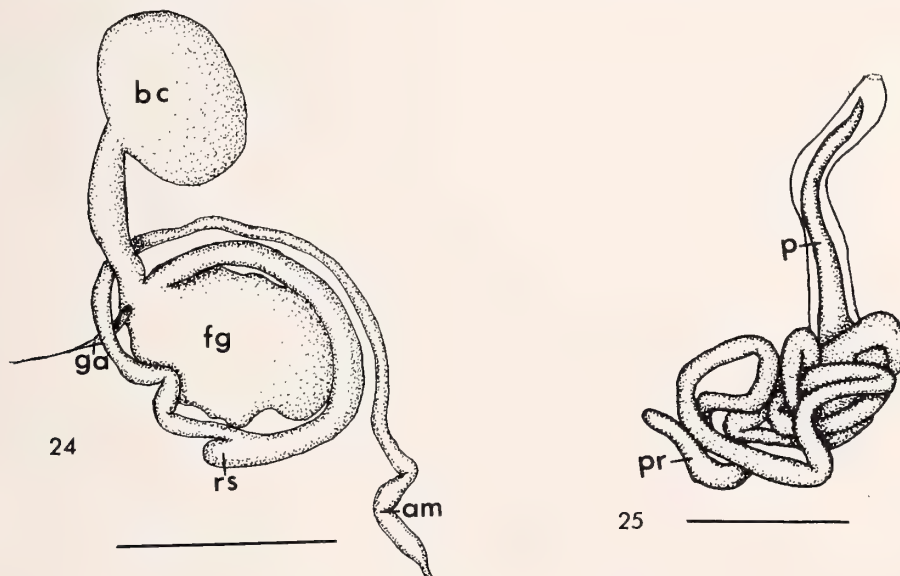
The present material of *Gastropteron rubrum* is well within the range of variation previously described for the species, with a few minor exceptions (Table 1). In one specimen there were as many as 28 denticles on the inner lateral tooth and in another specimen there were only 17 rows of radular teeth. The two western Atlantic specimens have 10 or 11 gill filaments which is fewer than previously reported.

Gastropteron vespertilium is exceedingly similar to *G. rubrum* in much of its external and internal morphology.

Gastropteron vespertilium is reproductive at 3 mm in length and reaches a maximum length of 5 mm. The two small individuals of *G. rubrum* from the western Atlantic were 2.5 and 3 mm in length, but were not fully mature. The penis was well developed but the female gland mass had not yet undergone differentiation. *Gastropteron rubrum* is known to reach a length of 24 mm (VAYSSI RE, 1880). The jaws and radulae of *G. vespertilium* and *G. rubrum* provide little basis for the separation of the species (Figures 10 to 15 and 19 to 22). There is considerable overlap in radular formulae and in the number of denticles on the inner lateral teeth. The number of gill filaments is similar in *G. vespertilium* and in specimens of *G. rubrum* of comparable size. The central nervous system is virtually identical in both species (VAYSSI RE, 1880; BERGH, 1893; present study).

The major differences between *Gastropteron vespertilium* and *G. rubrum*, other than the obvious and consistent differences in coloration, are in the shape of the shell and the reproductive morphology. In *G. vespertilium* the inner margin of the shell (Figure 23) is entire, whereas in *G. rubrum* there is a deep sinus.

The reproductive system has been completely described in only three species of *Gastropteron* (GUIART, 1901; MACFARLAND, 1966; GOSLINER, in press). In *G. rubrum* a semi-serial receptaculum seminis is absent but a serial receptaculum, which appears as a swelling of the hermaphroditic duct (Figure 24), is present in all described material (BERGH, 1893; GUIART, 1901; present study). In the two specimens of *G. vespertilium* that we examined, the hermaphroditic duct lacks either a serial or semi-serial



Explanation of Figures 24 and 25

Gastropteron rubrum (Rafinesque, 1814). Figure 24. Reproductive system: am, ampulla; bc, bursa copulatrix; fg, female gland mass; ga, genital aperture; rs, receptaculum seminis. Scale = 2.0 mm. Figure 25. Penis: p, penis; pr, prostate. Scale = 3.0 mm.

receptaculum and is of a uniform diameter throughout its length.

The structure of the penis also differs significantly between the two species (Figures 17 and 25). In *Gastropteron rubrum* (BERGH, 1893; GUIART, 1901; MARCUS & MARCUS, 1966) there is a narrow elongate prostate that consists of numerous convolutions. The penial papilla is elongate and conical. In *G. vespertilium* the prostate is thick and curved, but not convoluted. A distinct spermatic bulb is present. The penial papilla is exceedingly short and bifid at its apex.

Despite the similarities between *Gastropteron vespertilium* and *G. rubrum* in many aspects of their external and internal anatomy, the striking differences in coloration and the morphology of the shell, hermaphroditic duct, and penis ensures that they are distinct species. Although both species are found in the western Atlantic of Florida, they may not be sympatric. *Gastropteron rubrum* is known from the Atlantic coast of Florida to Brazil, but no confirmed reports exist from the Gulf of Mexico. *Gastropteron vespertilium* has only been collected in Tampa Bay, on the Gulf coast of Florida, but is likely to be more widespread.

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Numerous individuals and institutions provided substantial assistance at various stages in the completion of this work, including Sally D. Kaicher, Harold Humm, Susan and John Gallagher, Gale Sphon, Eveline Marcus, William Lyons, Johanna Reinhart, George Reid, the late Francis and Emily Smith, George W. Torrance, R. Tucker Abbott, Joseph Rosewater, Rod Armes, Robert Robertson, Nelson Cooley, Edward Petuch, Alan Bebbington, Vera Fretter, Victor Krantz, and the Museum National d'Histoire Naturelle, and the libraries of University of South Florida, Eckerd College, and the Florida State Board of Natural Resources, St. Petersburg Marine Research Laboratory. To them, we extend our sincere appreciation.

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Notes on the Tergipedid Nudibranchs of the Northeastern Pacific, with a Description of a New Species

by

DAVID W. BEHRENS

Pacific Gas & Electric Co., Biological Research Laboratory,
P.O. Box 117, Avila Beach, California 93424

Abstract. In the northeastern Pacific the family Tergipedidae is represented by 14 described species and at least 1 known undescribed species. The nomenclatural status of the family is reviewed and a new species, *Catriona rickettsi* Behrens, from California is described.

THE SYSTEMATICS of the family Tergipedidae Thiele, 1931, have experienced considerable controversy and nomenclatural confusion. Its taxonomic evolution has been reviewed by BURN (1973), MILLER (1977), and WILLIAMS & GOSLINER (1979). Modifications have followed with BROWN (1980), GOSLINER (1981), and GOSLINER & GRIFFITHS (1981). In the northeastern Pacific, species accounts are reported by MACFARLAND (1966), ROLLER (1969), LONG (1969), GOSLINER & MILLEN (1984), and JAECKLE (1984).

The generic status of *Catriona* Winckworth, 1941, *Cuthona* Alder & Hancock, 1855, and *Trinchesia* Ihering, 1879, has changed several times. MILLER (1977) found no clear separation between the genera. WILLIAMS & GOSLINER (1979) reestablished *Catriona* as a valid genus based upon the presence of bristles on the masticatory border of the jaw and the possession of more than 50 radular teeth. They also reported the family name Tergipedidae inappropriate and recommended Cuthonidae. BROWN (1980), while reviewing the British species, revised Williams & Gosliner on both these matters, following the nomenclature of MILLER (1977). GOSLINER & GRIFFITHS (1981), while not discussing Brown's revision, reemphasized the features separating *Catriona* from *Cuthona*, and stressed the importance of preradular teeth in *Catriona*.

Notes on the Tergipedidae of the Northeastern Pacific

Table 1 summarizes the tergipedid species known from the northeastern Pacific, and for which accurate collection data and/or voucher material is available. The list gives

the known geographical distribution of each species and the authors reporting those range limits.

THOMPSON & BROWN (1976) report "one doubtful record of" *Cuthona nana* (Alder & Hancock, 1845-55) from the Pacific coast of North America. No confirmable collection of *C. nana* is known from this coast. HURST (1967) reported *Catriona gymnota* (Couthuoy, 1838) (= *Catriona aurantia* Alder & Hancock, 1842) (*vide* WILLIAMS & GOSLINER, 1979; BROWN, 1980) from the vicinity of Friday Harbor Marine Laboratories, San Juan Island, Washington. ROBILLIARD (1971) documented collections of *Catriona columbiana* from this area, but not *C. gymnota*. Whereas the type locality of *C. columbiana* is Gabriola Pass, Vancouver Island region, British Columbia, and *C. gymnota* has not been reported since HURST (1967), it should probably be considered a misidentification.

BEHRENS (1980a:104) included four additional unidentified tergipedid nudibranchs. One, the La Jolla aeolid (species No. 158) remains undescribed. *Tergipes* sp. (species No. 160) has subsequently been described as *Cuthona phoenix* Gosliner, 1981.

The Lake Merritt aeolid (BEHRENS, 1980a:104, species No. 154) has also been listed by McDONALD & NYBAKKEN (1980:64) as *Cuthona* species A, and by McDONALD (1983:169) as *Trinchesia* sp., both from San Francisco Bay, California. This species was collected from Lake Merritt in 1967 by Dr. James T. Carlton. Subsequent to the publication of the color photograph in BEHRENS (1980a), Dr. Terrence Gosliner and Mr. Robert Burn brought to my attention the striking similarity between this species and *Cuthona perca* (Er. Marcus, 1958). *Cuthona perca* has been reported from an extremely wide geographical area, including Brazil (ER. MARCUS, 1958), Jamaica (EDMUNDS, 1964), Florida (EV. MARCUS, 1972), Barbados (MARCUS

Table 1

List of northeastern Pacific Tergipedidae.

- Cuthona* Alder & Hancock, 1855
- C. abronia* (MacFarland, 1966): Mukkaw Bay, Washington (ROBILLIARD, 1971)—Santa Catalina Island, California (JAECKLE, 1983)
- C. albocrusta* (MacFarland, 1966): San Juan Island, Washington (HURST, 1967)—Palos Verdes, California (MCDONALD, 1983)
- C. cocochroma* Williams & Gosliner, 1979: Trinidad Bay, Humboldt Co. (JAECKLE, 1984)—Duxbury Reef, Marin Co., California (WILLIAMS & GOSLINER, 1979)
- C. concinna* (Alder & Hancock, 1843): Brandon Island near Nanaimo, Vancouver Island, British Columbia (O'DONOGHUE, 1922), Circum-polar
- C. divae* (Marcus, 1961): San Juan Islands, Washington (ROBILLIARD, 1971)—Point Loma, California (HAMANN, 1981)
- C. flavovulta* (MacFarland, 1966): Palmer's Point, Humboldt Co. (JAECKLE, 1984)—Shell Beach, San Luis Obispo Co., California (ROLLER & LONG, 1969)
- C. fulgens* (MacFarland, 1966): Duxbury Reef, Marin Co. (GOSLINER & WILLIAMS, 1970)—Shell Beach, San Luis Obispo Co., California (LONG, 1969)
- C. lagunae* (O'Donoghue, 1926): Palmer's Point, Humboldt Co., California (JAECKLE, 1984)—Punta Cabras, Mexico (HAMANN, 1981)
- C. perca* (Marcus, 1958): San Francisco Bay and Lake Merritt, Oakland, California (present study), Brazil (MARCUS, 1958), Jamaica (EDMUNDS, 1964), Florida (EV. MARCUS, 1972), Barbados (MARCUS & HUGHES, 1974), New Zealand (MILLER, 1977), Hawaii (GOSLINER, 1980)
- C. phoenix* Gosliner, 1981: Morro Bay (BEHRENS, 1980a), Mission Bay (GOSLINER, 1981) and La Jolla, California (BEHRENS, 1980a)
- C. pustulata* (Alder & Hancock, 1845): Salt Spring Island, Galiano Island, Strait of Georgia, British Columbia, Canada, and the northeastern Atlantic (GOSLINER & MILLEN, 1984)
- C. virens* (MacFarland, 1966): Duxbury Reef, Marin Co. (MCDONALD & NYBAKKEN, 1980)—Santa Catalina Island, California (JAECKLE, 1983)
- C. species 1*: La Jolla, California (J. Lance, personal communication)
- Catriona* Winckworth, 1941
- C. columbiana* (O'Donoghue, 1922): Pearse Island, British Columbia (LAMBERT, 1976)—San Diego, California (LANCE, 1966), Japan (BABA & HAMATANI, 1963), South Africa (GOSLINER & GRIFFITHS, 1981)
- C. rickettsi* Behrens, spec. nov.: San Francisco Bay, California (present study)
- Tenellia* Costa, 1877
- T. adspersa* (Nordmann, 1845): San Francisco Bay (STEINBERG, 1963)—Morro Bay, California (MCDONALD & NYBAKKEN, 1980), Europe, New England

& HUGHES, 1974), and New Zealand (MILLER, 1977) as *C. reflexa*, and Hawaii (GOSLINER, 1980).

The San Francisco Bay specimens match identically descriptions given in MILLER (1977) and GOSLINER (1980) for *Cuthona perca*. The radular length of 28 teeth fits well

within the range of 16 to 35 reported in the above references. GOSLINER (1980) reports 11 denticles per tooth. The San Francisco Bay specimens bear 5–10 denticles per tooth. The radular drawing presented in MCDONALD (1983) matches closely that shown in GOSLINER (1980) for the Hawaiian specimens. The coloration of the specimens also matches closely that previously reported. The body is translucent grayish-white with white specks. The cerata bear numerous opaque white specks and a similarly colored subapical white band. The ceratal cores are olive-green.

The two localities where this species has been collected in California are a tidal lagoon, which due to its distance from the shore of San Francisco Bay is called a "lake," and the Palo Alto Yacht Harbor, South San Francisco Bay (BEHRENS, 1980b; MCDONALD & NYBAKKEN, 1980; MCDONALD, 1983). Both water bodies exhibit marked differences from California coastal waters; during the summer months they are quite warm and highly saline. The feasibility of the introduction of species such as *Cuthona perca* is discussed by CARLTON (1975, 1978, 1979) and MILLER (1969). At each of these localities, this species was feeding on the same sea anemone species, the introduced Asian anemone, *Halipanella luciae* (Verrill, 1898) (MCDONALD, 1983; present study).

The fourth species listed in BEHRENS (1980a:104), *Trinchesia* sp. (species No. 161), is described in this paper. It was originally reported by BEHRENS & TUEL (1977), after being collected in San Francisco Bay in 1974. This *Catriona* is one of the most abundant aeolidacean species occurring year-round in south San Francisco Bay. Specimens have also been collected in La Jolla, California by Mr. James R. Lance.

Family TERGIPEDIDAE Thiele, 1931

Catriona Winckworth, 1941*Catriona rickettsi* Behrens, spec. nov.

(Figures 1 to 7)

References and synonymy:

- Trinchesia* sp.: BEHRENS & TUEL, 1977:35. CARLTON, 1979: 432. BEHRENS, 1980a:37. BEHRENS, 1980b:104.

Type material: (1) Holotype: One specimen approximately 13 mm long (preserved) collected from boat floats at Pete's Harbor, Port of Redwood City, San Francisco Bay, California (Lat. 37°30'02"N; Long. 122°13'23"W) on December 24, 1981, by David W. Behrens. This specimen is deposited in the collection of the California Academy of Sciences, Departments of Invertebrate Zoology and Geology (CAS), San Francisco, California (CAS Catalogue No. 029323). (2) Paratypes: A series of six specimens 8–15 mm long (preserved) collected concurrently with the holotype is also deposited in the CAS collection, Catalogue No. 029324. (3) A series of six specimens 6–9 mm long (preserved) collected at the type locality on April

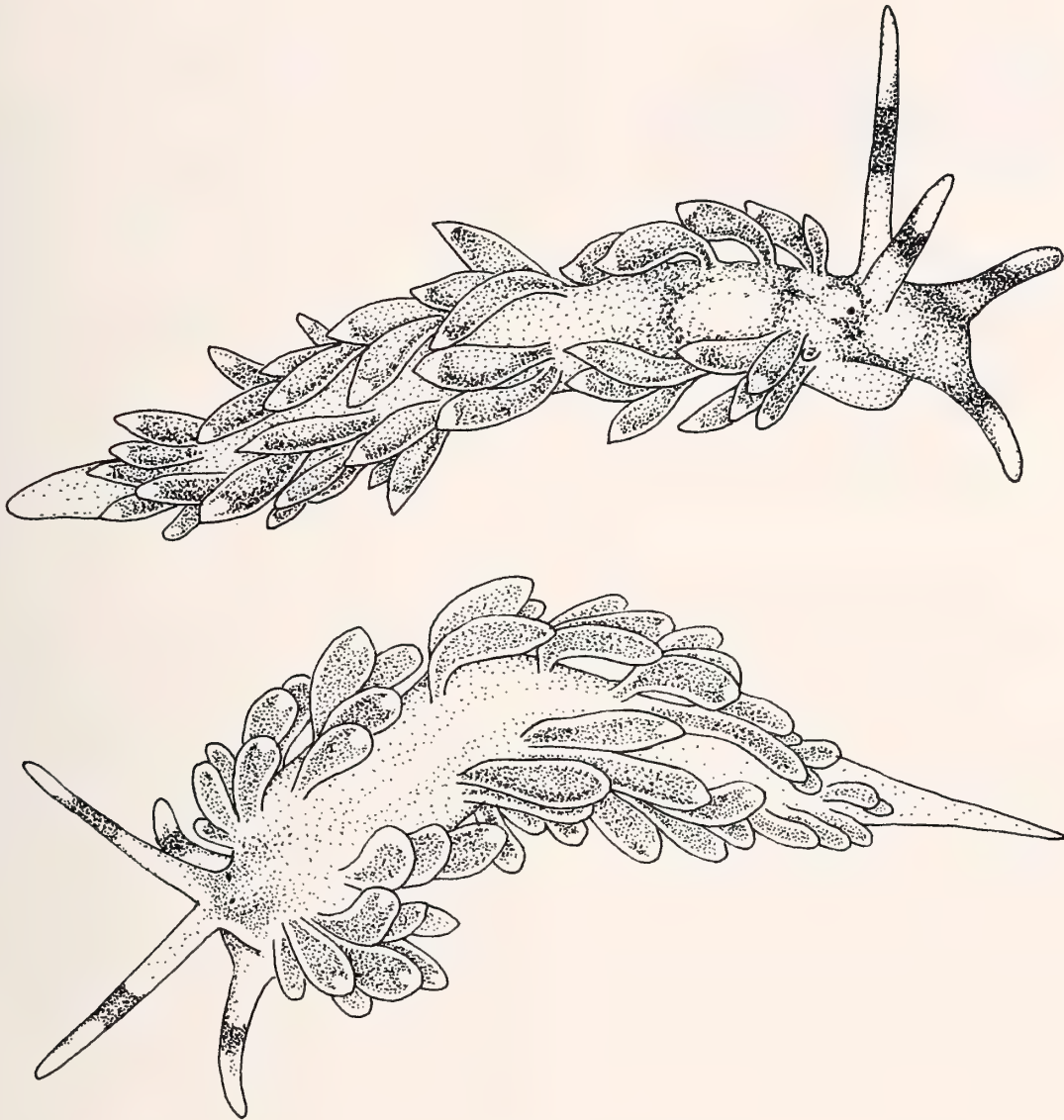


Figure 1

Catriona rickettsi spec. nov. Two specimens, each 18 mm in length. Pete's Harbor, Port of Redwood City, San Francisco Bay, California. Drawn from color transparencies.

18, 1981, is deposited in the type collection of Los Angeles County Museum of Natural History (LACM). Color transparencies of living *Catriona rickettsi* are on file at CAS (Nos. 3749, 3750 and 3751) and LACM.

Other material examined:

- (1) 18 specimens, Pete's Harbor, Port of Redwood City, San Mateo County, California; leg. David W. Behrens, 24 September 1974.
- (2) 20 specimens, Pete's Harbor, Port of Redwood City, San Mateo County, California; leg. David W. Behrens, 23 November 1978.
- (3) 12 specimens, Pete's Harbor, Port of Redwood City, San Mateo County, California; leg. David W. Behrens, 12 August 1979.
- (4) 25 specimens, Pete's Harbor, Port of Redwood City, San Mateo County, California; leg. David W. Behrens, 27 November 1980.
- (5) 15 specimens, Pete's Harbor, Port of Redwood City, San Mateo County, California; leg. David W. Behrens, 18 April 1981.
- (6) 20 specimens, Pete's Harbor, Port of Redwood City, San Mateo County, California; leg. David W. Behrens, 26 November 1981.

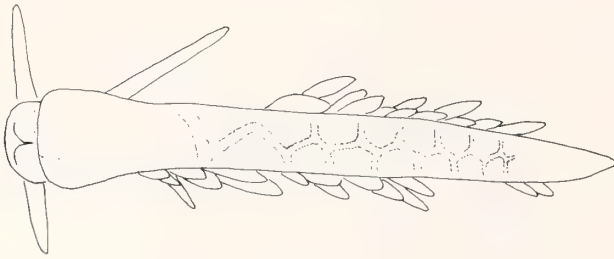


Figure 2

Ventral view of *Catriona rickettsi* spec. nov. 16 mm length. Pete's Harbor, Port of Redwood City, San Francisco Bay, California. Drawn from color transparency.

- (7) 18 specimens, Pete's Harbor, Port of Redwood City, San Mateo County, California; leg. David W. Behrens, 24 December 1981.

Description: The living animals measured up to 20 mm in length. Body is long, slender, tapering posteriorly. Tail is about $\frac{1}{5}$ the body length (Figure 1). The anterior portion of the foot flares slightly and is rounded (Figure 2). The foot is roughly $\frac{1}{10}$ as wide as long. The oral tentacles are long and slender and about $\frac{3}{4}$ the length of the rhinophores (Figure 1). The rhinophores are long, about $\frac{1}{5}$ – $\frac{1}{6}$ the length of the body, smooth to very slightly verrucose, and tapering. The cerata are arranged in 8–10 rows, the longest of which bears up to six cerata. There are up to four rows of cerata in the prepericardial group. Postpericardial rows alternate. A typical ceratal arrangement was 2.3.4 (prepericardial) and 5.6.3.1.1 (postpericardial). A single ceras (Figure 3), when fully extended, is approximately $\frac{1}{5}$ – $\frac{1}{6}$ the length of the body. Ceratal shape varies greatly from fusiform to a more club shape. The anus lies immediately in front of the dorsal-most ceras of the first postpericardial row. The genital apertures lie on the right side of the body, ventral to the first and second anterior rows of cerata.

The body is translucent, allowing many of the organs to be seen. In some larger specimens, the region between the rhinophores and the pericardium is yellow to orange. There is opaque white pigment on the distal $\frac{1}{3}$ of the rhinophores and cephalic tentacles and at the apex of the cerata. On the tentacles, this pigmentation is restricted to

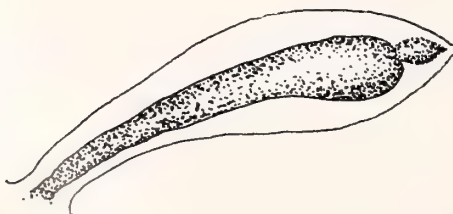


Figure 3

Ceras from *Catriona rickettsi* spec. nov.

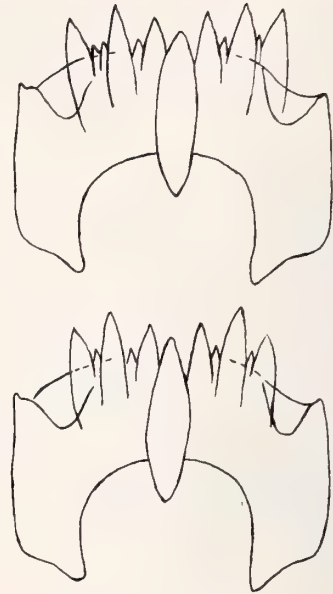


Figure 4

Radular teeth of *Catriona rickettsi* spec. nov.

the dorsal surface. An occasional white speck may occur on the surface of the cerata or on the notum. A band of orange is found below the white apices of the rhinophores and cephalic tentacles. This band may be nearly indiscernible on the tentacles in some individuals. The color of the ceratal core varies greatly, from yellow through orange, pink, red-brown, burgundy, or brownish-green. In some specimens the color may gradate from greenish, proximally, to reddish-brown below the white cap. A color

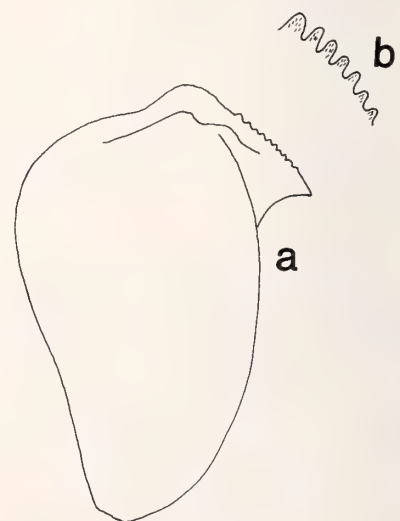


Figure 5

Jaw of *Catriona rickettsi* spec. nov. a, lateral view of jaw. b, masticatory border.



Figure 6

Penis of *Catriona rickettsi* spec. nov.

photograph of a specimen with orange cerata can be found in BEHRENS (1980a:105).

The long, tapering uniseriate radula is composed of up to 75 teeth, including three preradular teeth. Each tooth is a low horseshoe-shaped arch, with a deep articulatory socket on either side (Figure 4). The central cusp forms a long ridge that extends slightly below the blade of the tooth. There are 3–5 large denticles to each side of the cusp, three of which project further than the central cusp itself. One or two small denticles may be found between the larger ones (Figure 4). The consistency of these smaller denticles was confirmed using scanning electron microscopy (SEM). The jaws (Figure 5a) are lightly tinted gold, thin and oval. The masticatory process has a series of coarse denticles, with faintly discernible bristles (Figure 5b).

The reproductive system was typically tergipedid. The hermaphrodite glands are large, spherical to oval, tightly covered with elongated, inflated peripheral female acini. They extend posteriorly to the last division of the digestive gland and discharge into a median hermaphrodite duct. The ampulla is very long and convoluted. The vas deferens is very short. The penial gland is long, recurved and slightly inflated at its distal end. The penis is short, conical, and blunt (Figure 6). Upon dissection and clearing with 0.5 N quaternary ammonium hydroxide, it was found to be unarmed.

In South San Francisco Bay, *Catriona rickettsi* has been collected from a variety of fouling communities. Egg masses are present year-round, indicating the presence of this small, highly cryptic tergipedid. The egg mass (Figure 7) is typical of Type D (HURST, 1967), being an irregularly twisted, clear gelatinous string housing a spiral or folded string of white-cream eggs. A large egg string contains 12–30 eggs in cross-section (Figure 7b), with one egg per capsule. The mass is attached to the substratum, usually the stalk of a hydroid, by a very thin capsule-free jelly sheet. An average tangled mass measures about 2 by 6 mm.

The preferred substratum of this species seems to be *Tubularia crocea* (Agassiz, 1862), the hydranth of which the aeolid closely resembles, both in color and form. Other cnidarian species common in this locality are *Obelia* sp. and *Halipanelia luciae*, the latter of which also closely resembles the ceratal morphology of *Catriona rickettsi*.

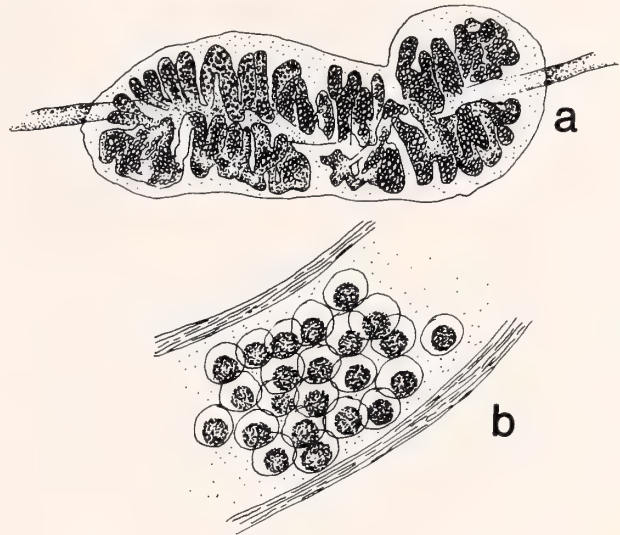


Figure 7

Egg mass of *Catriona rickettsi* spec. nov. a, whole egg mass (6 mm long) attached to hydroid stalk. b, view of single strand of egg string within a mass. Drawn from color transparency.

Discussion: Eight species are assigned to the genus *Catriona* based upon a long, tapering radula of greater than 50 teeth and the presence of a preradular tooth (GOSLINER & GRIFFITHS, 1981). Until this study, only Miller's *C. alpha* from New Zealand lacked a penial stylet. All species except *C. oba* Marcus, 1970, bear bristles on the masticatory edge of the jaw. Limited by these characteristics, assignment of *C. rickettsi* to this genus seems most appropriate.

Catriona maua Marcus & Marcus, 1960, and *C. oba* differ from *C. rickettsi* in that they bear a red line on the rhinophores. *Catriona gymnota* (Couthouy, 1938), *C. tema* Edmunds, 1968, and *C. casha* Gosliner & Griffiths, 1981, differ from *C. rickettsi* in having a subapical white band on the cerata. These species also have geographic distributions far from that of *C. rickettsi*.

In the northeastern Pacific, *Catriona rickettsi* most closely resembles *Catriona columbiana* (O'Donoghue, 1922). Differences in surface pigmentation (a highly consistent character in this genus), radular dentition, penial armature, structure of the masticatory border of the jaw, and the egg mass set the two sympatric species apart.

WILLIAMS & GOSLINER (1979) synonymized *Catriona alpha* Baba & Hamatani, 1963, with *C. columbiana*. The primary similarity was that of coloration. The particular features of coloration have been stressed by several authors. BABA & HAMATANI (1963) report in their description of the species that the holotype had "opaque white dots on the head region . . . and on nearly the whole length of the branchial papillae on their surface." They report also that the paratype had branchial papillae with an outer longitudinal, opaque-white line. MACFARLAND

(1966) in describing *C. columbiana* (as *C. spadix*) reports that the cerata bear a broad frosted-white band extending from base to tip. McDONALD (1983) describes the coloration of the species similarly. GOSLINER & GRIFFITHS (1981) report *C. columbiana* from South Africa. In their specimens, opaque white pigmentation covered the surface of the cerata, spreading to the notal surface. They report that the coloration agrees with that of the holotype of *C. alpha*, stating that, within the geographical range of *C. columbiana*, the external opaque white occurs over the whole surface or is restricted to a white longitudinal line or subapical band on the cerata. LANCE (1966), while reporting its collection in southern California, states that the color pattern of this species is distinct, enabling it to be readily distinguished from other aeolid nudibranchs. He reports that the antero-dorsal surface of all cerata, except the smallest, is covered with a highly contrasting, intense opaque-white pigment. The pigment was also present on the dorsal surface of the head as a triangular patch (LANCE, 1966; also see BEHRENS, 1980a:84). GOSLINER & MILLEN (1984) distinguish *C. columbiana* from all other sympatric species in Canadian waters by the white opaque ceratal line. *Catriona rickettsi* has none of the above-mentioned color patterns.

GOSLINER & GRIFFITHS (1981; fig. 15) present a comparison of the radular teeth of *Catriona*. Although striking differences occur between the four examples of *Catriona columbiana* presented (after O'DONOGHUE, 1922; BABA & HAMATANI, 1963; MACFARLAND, 1966; and GOSLINER & GRIFFITHS, 1981), the denticulation and morphology described here for *C. rickettsi* (3–5 large denticles between which lie 0–2 smaller denticles) remain substantially different enough for the purpose of species separation.

In the original description, O'DONOGHUE (1922) did not illustrate the penis or stylet of *Catriona columbiana*. In *C. rickettsi* the penis is short and blunt, not elongate and tapering as shown for any of the examples of *C. columbiana* given in GOSLINER & GRIFFITHS (1981). Additionally, the presence of a penial stylet was not described by BABA & HAMATANI (1963) for *C. columbiana* (as *C. alpha*). ROLLER (1969) confirmed the presence of a penial stylet in the Japanese *C. columbiana*. *Catriona rickettsi* has no such penial armature.

GOSLINER & GRIFFITHS (1981) describe the bristles on the denticles of the masticatory border of the jaw as large and clearly defined; ROLLER's (1969) description is similar. In *Catriona rickettsi*, the bristles are faintly discernible. This interspecific difference was confirmed by Dr. Kikutarô Baba (personal communication).

The egg mass of *Catriona columbiana* is a bag-like sac (Sandra Millen, personal communication) and not a spiral or folded string as is described here for *C. rickettsi* and is more typical of tergipedid nudibranchs (HURST, 1967).

MILLER (1977) identified specimens as *Catriona alpha* from New Zealand. His specimens reportedly differ from the Japanese specimens in a manner similar to the species from south San Francisco Bay described here. GOSLINER

& GRIFFITHS (1981), while comparing New Zealand material with that from South Africa and California, amplify the described differences between Miller's species and *C. columbiana*. The reported ceratal variability, lack of characteristic white markings, and lack of penial stylet closely match characters described here for *Catriona rickettsi*. Miller's specimens, however, lack bristles on the masticatory border of the jaw. Further examination of the New Zealand species is required to confirm its status.

The trivial name *rickettsi* is given in honor of Edward F. Ricketts (1897–1948) for his outstanding contributions in the field of philosophy and to our understanding of intertidal ecology. HEDGPETH (1978a, b) presents a chronology of the life of Ricketts, highlighting the man and his contributions.

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The Morphology, Reproduction and Ecology of the Commensal Bivalve *Scintillona bellerophon* spec. nov. (Galeommatacea)

by

DIARMAID Ó FOIGHIL AND ALLAN GIBSON

Department of Biology, University of Victoria,
Victoria, British Columbia V8W 2Y2, Canada

Abstract. *Scintillona bellerophon* spec. nov. is ectocommensal with the holothurian *Leptosynapta clarki* (Heding, 1928) in Sooke Harbour, Vancouver Island, British Columbia. It is similar in form and habit to *Scintillona zelandicus* (Odhner, 1924) and is a simultaneous hermaphrodite with a fecundity of up to 3000 eggs. The young are brooded in the suprabranchial chamber and released as D-veligers. Following a planktotrophic stage, settlement and subsequent attachment to the host species occurs. In aquaria, attached animals locate deeper in the sediment than unattached specimens. Individuals may live up to 4 years. Another galeommatacean bivalve, *Mysella tumida* (Carpenter, 1864), and two polychaete species are associated with *L. clarki* in Sooke Harbor. Both *S. bellerophon* and *S. zelandicus* are relatively less specialized than related bivalves ectocommensal on holothuroids.

INTRODUCTION

THE SUPERFAMILY Galeommatacea contains numerous species that live in association with a large diversity of host species. Some members of the genera *Entovalva*, *Devonia*, *Cycladoconcha*, *Montacuta*, and *Scintillona* occur on or in synaptid holothurian hosts (Boss, 1965). In September 1982, an intertidal population of an unidentified bivalve was found in Sooke Harbour, Vancouver Island, British Columbia. Specimens recovered were attached externally to the synaptid holothuroid *Leptosynapta clarki* (Heding, 1928). The bivalve was identified as a new species of *Scintillona*, and is the first record of this genus on the Pacific coast of North or South America. It is similar in form and habit to *S. zelandicus* (Odhner, 1924), but differs in details of the shell, foot and mantle. *Scintillona zelandicus* occurs off New Zealand to depths of 90 m (ODHNER, 1924) and intertidally as an ectocommensal attached to the synaptid *Trochodonta dendyi* Mortensen (MORTON, 1957). Its morphology has been described from preserved specimens by ODHNER (1924) and from live animals by MORTON (1957), who also made behavioral observations. *Scintillona stigmatica* (Pilsbry, 1920) has been recorded off Hawaii (PILSBRY, 1920), and attached to the echinoid *Brissus lateracarinatus* (Leske) off Japan (YAMAMOTO & HABE, 1974).

Galeommataceans exhibit a wide variety of reproductive specializations and are generally considered to have the most complex reproductive patterns in the Bivalvia (DEROUX, 1961; JENNER & McCARY, 1968; MORTON, 1976; OCKELMANN & MUUS, 1978). There is no available information concerning reproduction in *Scintillona*. Therefore, aspects of the reproduction of *S. bellerophon* spec. nov., as well as the morphology and ecology, are described.

MATERIALS AND METHODS

Animals were sampled intertidally at Woodward Point in Sooke Harbour (Figure 1). Sampling was carried out monthly during spring tides from October 1982 to April 1983 as well as in June and September 1983. All specimens of *Leptosynapta clarki* encountered were removed from their burrows and examined in the laboratory with a dissecting binocular microscope. Specimens of *Scintillona bellerophon* were removed from the holothuroids, measured with an ocular micrometer, and checked for the occurrence of brooding. Individuals were fixed for light-microscope histology in 4% glutaraldehyde (biological grade), dehydrated in ethanol, embedded in Poly Bed 812, sectioned at 1 μ m and stained with Richardson's stain (RICHARDSON & JARRET, 1960). For scanning electron



Figure 1

Location of Woodward Point, Sooke Harbour, British Columbia, type locality and study area of *Scintillona bellerophon* spec. nov.

microscopy, specimens were fixed in a 3:1 mixture of 4% glutaraldehyde and 1% osmium tetroxide in 3% NaCl (SMITH, 1983), dehydrated in acetone, critical point dried, gold coated, and viewed with a JEOL JSM-35 scanning electron microscope.

SYSTEMATICS

Family GALEOMMATIDAE Gray, 1840

Genus *Scintillona* Finlay, 1927

Small shells, being rounded at both ends. Small tubercular cardinal tooth in right valve; oblique cardinal in left, extending into a thin lamella. Resilium has a prominent nymph (CHAVAN, 1969).

Type species: *Scintillona zelandicus* (Odhner, 1924) (by original designation, *Spaniorinus zelandicus* Odhner, 1924).

Scintillona bellerophon
Ó Foighil & Gibson, spec. nov.

(Figures 1 to 14)

Specific characteristics: Umbone slightly posterior, mid-mantle fold extended posterodorsally as three pairs of retractable flaps; distal part of foot has prominent longitudinal ciliated grooves.

Type location: Woodward Point, Sooke Harbour, Vancouver Island, British Columbia, Canada (48°21'49"N; 123°42'54"W).

Holotype: British Columbia Provincial Museum, Victoria, British Columbia (BCPM) 983-1617-1. **Paratypes:** BCPM 983-1617-2, National Museum of Natural Sciences, Ottawa (NMNS) 86701 and NMNS 86702 (Table 1).

RESULTS

Morphology

The valves are broadly elliptical (Figure 2) ranging up to 4.4 mm in length. They are equivalve and non-equi-

Table 1

Shell dimensions (mm) of holotype and paratypes of *Scintillona bellerophon* spec. nov.

Specimen	Length	Height	Width
Holotype BCPM 983-1617-1	4.2	2.7	1.7
Paratype BCPM 983-1617-2	2.1	1.5	0.7
Paratype NMNS 86701	3.7	2.4	1.2
Paratype NMNS 86702	3.3	2.2	1.1



Figure 2

Right valve of *Scintillona bellerophon* spec. nov. showing deposit (d).

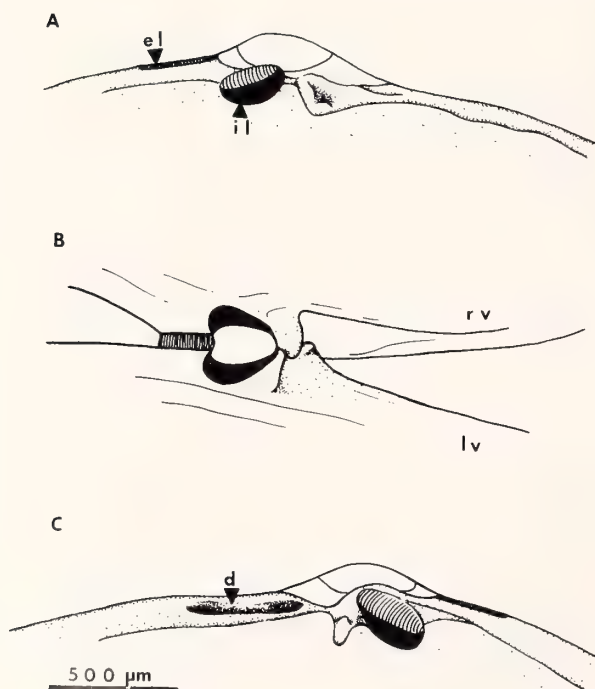


Figure 3

Scintillona bellerophon spec. nov.: A. Hinge of left valve; B. Ventral view of hinge; C. Hinge of right valve. d, depression; el, external ligament; il, internal ligament; lv, left valve; rv, right valve.

lateral, the orthogyrous umbone being slightly posterior ($\frac{3}{5}$ of the total shell length from the anterior) and having a prominent, rounded prodissoconch-2. The valve margins are excurved, particularly anterodorsally and to a lesser extent posterodorsally. As a result, the valves cannot be firmly apposed.

The outer shell surface appears slightly nacreous and is usually whitish in color. Fine concentric lines are present on the other outer shell surface, and in some individuals distinct growth checks are present. Many individuals display a prominent patch of dark brown or purple deposit (Figure 2) similar to that occurring on numerous other galeommataceans commensal with burrowing hosts (GAGE, 1966; KAWAHARA, 1942; MORTON, 1957; PILSBRY, 1920; PONDER, 1968). A prominent periostracal edge is present, especially anteriorly. Numerous pits (visible at $\times 40$ magnification) occur on the inner surface of the shell. The pallial line is entire, and the anterior and posterior adductor muscle scars are of a similar size.

The external ligament is weak and posterior, and the internal ligament is moderately developed and has a marked nymph. In the left valve, a single, more robust anterior tooth occurs, and is connected to a lateral ridge (Figure 3A) that articulates with a corresponding shallow depression in the right valve (Figure 3C). A single peg-like tooth is present in the right valve (Figure 3C), the base of which is continuous with a weak ridge delineating the shallow depression. Both teeth are cyclodont and interlock across the hinge line (Figure 3B).

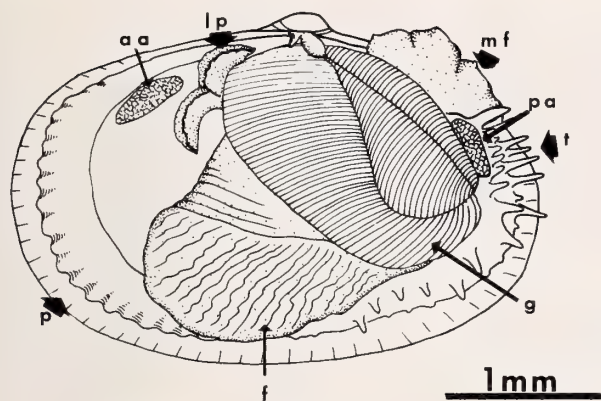


Figure 4

Scintillona bellerophon spec. nov. General morphology (left valve and left mantle fold removed). aa, anterior adductor muscle; f, foot; g, gill; lp, labial palps; mf, mid-mantle fold extension; p, periostracum; pa, posterior adductor muscle; t, inner mantle fold tentacles.

The inner fold of the mantle is fused posteroventrally to separate an anterior pedal (inhalent) opening from a narrow, slit-like posterior exhalent siphon. Anterior to the fusion, the inner fold has a scalloped margin. Numerous tentacles (20–30) are present on the region of fusion and surrounding the exhalent siphon. The edge of the mid-mantle fold bears small papillae, except dorsoposteriorly. Here the mid-fold is hypertrophied into three flaps on either side which, when relaxed, extend to cover the shell surface dorsal to the exhalent siphon. Ridges are present on the inner face of these flaps, but they do not display ciliary activity. The outer mantle fold is small and is attached to the periostracal edge.

The homorhabdic eulamellibranchiate ctenidia cover the visceral mass, with the gill axis (orientated at approximately 45° to the long axis) extending from under the umbone to the exhalent opening (Figure 4). Inner and outer demibranchs are present, as in other galeommatids (POPHAM, 1940); the outer demibranchs, however, are much reduced in size, especially anteriorly. A food groove is present in the inner demibranch only.

Ascending and descending lamellae are present in both demibranchs. In the outer demibranch, the ascending lamellae extend dorsally to fuse with the mantle above the gill axis. The inner demibranchs fuse behind the foot. Few interlamellar junctions occur, and these are restricted to the extreme posterior of the gill.

Gill ciliation is similar to that described for other galeommatids (JUDD, 1971; POPHAM, 1940). Particles are passed ventrally along the ascending lamellae of the outer demibranchs and dorsally via the descending lamellae to the gill axis. Here the particles are propelled anteriorly and then ventrally toward the labial palps. Ciliary currents on both lamellae of the inner demibranchs pass par-

ticles to the ventral food groove, and hence to the labial palps.

The foot is large and laterally compressed, and has two distinct parts (Figure 4). The distal portion is thickened and opaque, and has a pleated surface with 20–30 longitudinal, densely ciliated grooves. The proximal part is thinner, smooth-surfaced, and more translucent. The cilia in the distal grooves become active only when the foot is engaged in locomotion. Particles are passed dorsally along these grooves, bound in a mucous sheet, and pushed over the outer mantle fold when the foot contracts. A byssal gland is present at the posteroventral end of the distal section of the foot.

Locomotion is achieved as in *Scintillona zelandicus* (MORTON, 1957). The distal part of the foot is extended and applied laterally to the substratum. This is followed by serial contractions of the anterior, then posterior, pedal retractor muscles, which rock the rest of the body forward onto the foot. Byssal attachment is accomplished by adopting an upright position, contact with the substratum being made by the slender base of the foot onto which the byssal gland opens.

Waste particulate material in the mantle cavity is expelled anteriorly by valve contractions, or ventrally by mantle ciliary rejection tracts between the foot and the region of mantle fusion. Fecal pellets and brooded veliger larvae exit via the exhalent siphon.

The gonad develops along the ventral and posterior margins of the digestive gland. *Scintillona bellerophon* is a simultaneous hermaphrodite, with sperm and eggs developing within separate follicles (Figure 5). In individuals less than 2.5 mm in length, the gonad is predominantly male. The ovotestis is connected to the suprabranchial chamber by a pair of ciliated gonoducts, one on each side. Some specimens contained a few sporocysts of an unidentified helminth parasite embedded in the gonad.

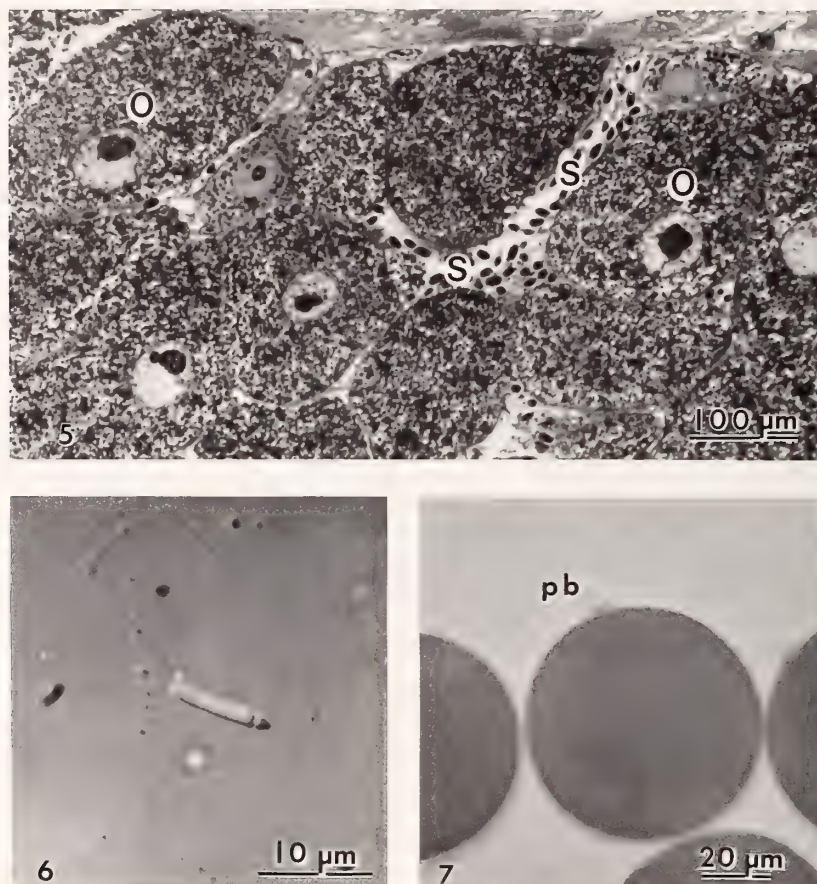
Reproduction

Fertilization occurs in the suprabranchial chamber and embryos are brooded there until they have reached the D-veliger (straight hinge) stage of development. They are then released and assume a planktotrophic existence until settlement. It is not known if *Scintillona bellerophon* self-fertilizes.

Brooding individuals were observed in the November 1982 and February–September 1983 samples, with the highest frequency of brooders in March and April of 1983 (38% and 10% respectively). Samples from the other months showed less than 2% of the animals brooding.

Uncleaved eggs observed in the gill chamber had undergone two reduction divisions (Figure 7) and are about 70 µm in diameter ($\bar{x} = 69.9 \pm 1.1$ SE, $n = 40$). The fecundity of three specimens examined ranged from 1965 (2.95 mm valve length) to 2912 (3.5 mm valve length).

The sperm heads are rodlike in shape and are 10 µm



Explanation of Figures 5 to 7

Scintillona bellerophon spec. nov. Figure 5. Light micrograph of the ovotestis. o, oocyte; s, spermatids. Figure 6. Light micrograph of sperm. Figure 7. Light micrograph of ovum. pb, polar bodies.

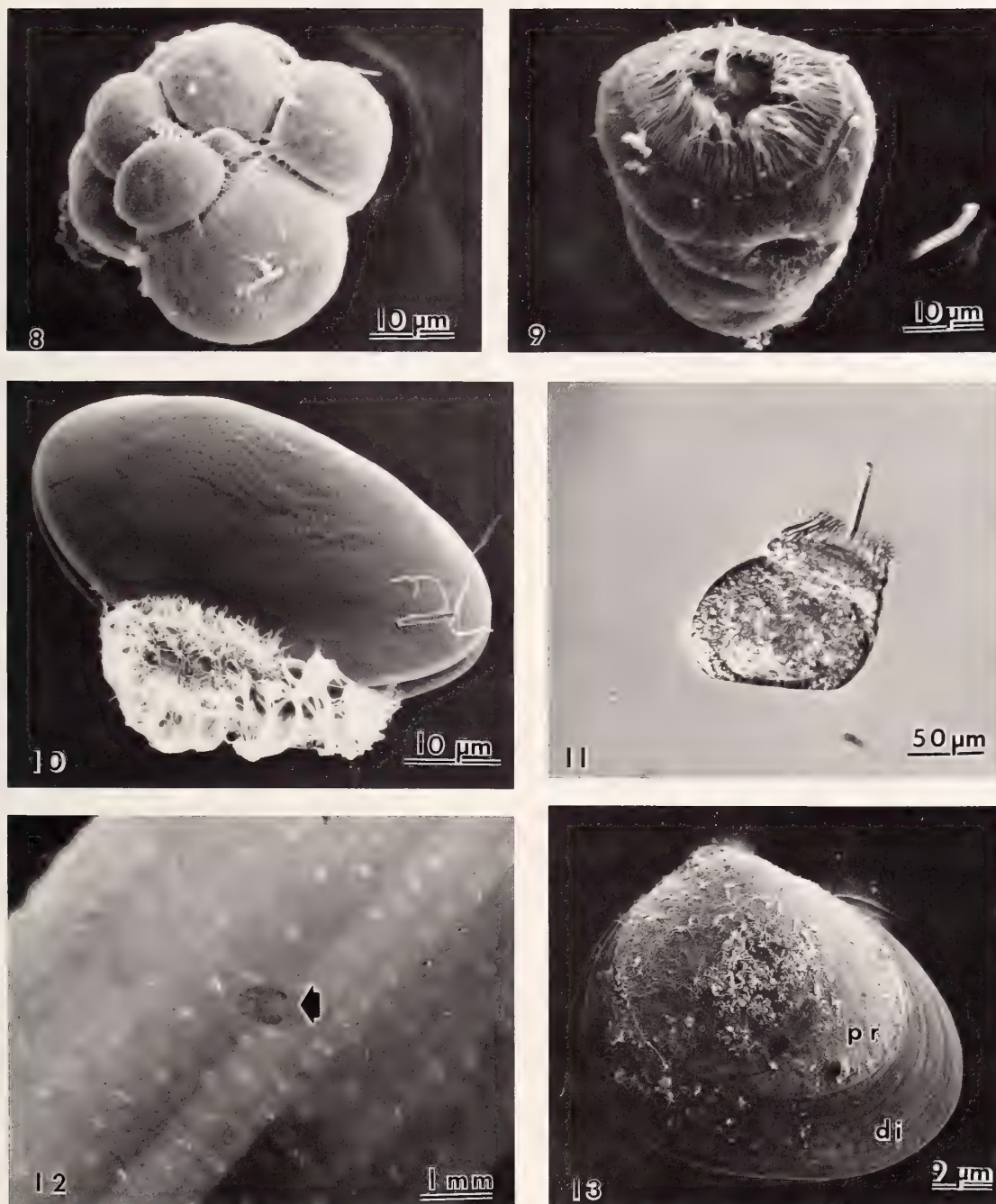
in length (Figure 6). They are generally similar to, though considerably shorter than, the eupyrene sperm of *Mysella bidentata* (Montagu, 1803) (OCKELMANN & MUUS, 1978). The sperm aggregate when removed from the gonad, forming large spherical masses as reported in *M. bidentata* by OCKELMANN & MUUS (1978).

Embryonic development from early cleavage stages to larval release took 12 days at 10°C in aquarium-held specimens (ambient water temperature in March 1983 was 10.3°C). No encapsulating fertilization membrane was apparent in early embryos (Figure 8). Ciliation appears at the trochophore stage (Figure 9), and the embryos are capable of weak swimming movements when removed from the gills. Early developmental stages are circulated by the adult around the gill chamber. As the embryos grow and develop valves, the gills become distended, inhibiting further embryo movement. Mature D-veligers have a rust-colored hinge line, which gives brooding animals a pink internal coloration as in *Montacuta percompressa* Dall, 1899

(CHANLEY & CHANLEY, 1970). The prodissoconch-1 of *Scintillona bellerophon* has a pitted surface (Figure 10). It also shows faint radial lines towards the margin as described by REES (1950) for the Galeommatacea (Erycinacea) and Lucinacea.

Mature D-veligers (Figure 11) are released through the exhalant siphon in a few pulses. They immediately commence vigorous swimming. Mean valve length at release was $130 \mu\text{m} \pm 2.1 \text{ SE}$, and mean valve height was $97 \mu\text{m} \pm 2.5 \text{ SE}$ ($n = 40$) (Figure 11). The duration of the larval stage was not determined.

Settlement occurs when the larvae are between 300 and 375 μm in length. Newly metamorphosed juveniles with little or no dissoconch growth were found attached to *Lepidosynapta clarki* (Figure 12). In aquaria, dislodged juveniles were frequently picked up by the feeding tentacles of the holothuroid and passed onto the host's body surface. Many of these reattached by byssal threads at the base of the tentacles. This is in contrast to *M. percompressa* where



Explanation of Figures 8 to 13

Scintillona bellerophon spec. nov. Figure 8. Scanning electron micrograph (SEM) of early morula. Figure 9. SEM of trochophore. Figure 10. SEM of D-veliger, before release. Figure 11. Light micrograph of newly released D-veliger. Figure 12. Newly settled *Scintillona bellerophon* attached to *Leptosynapta clarki*. Figure 13. SEM of juvenile. di, dissoconch; pr, prodissoconch.

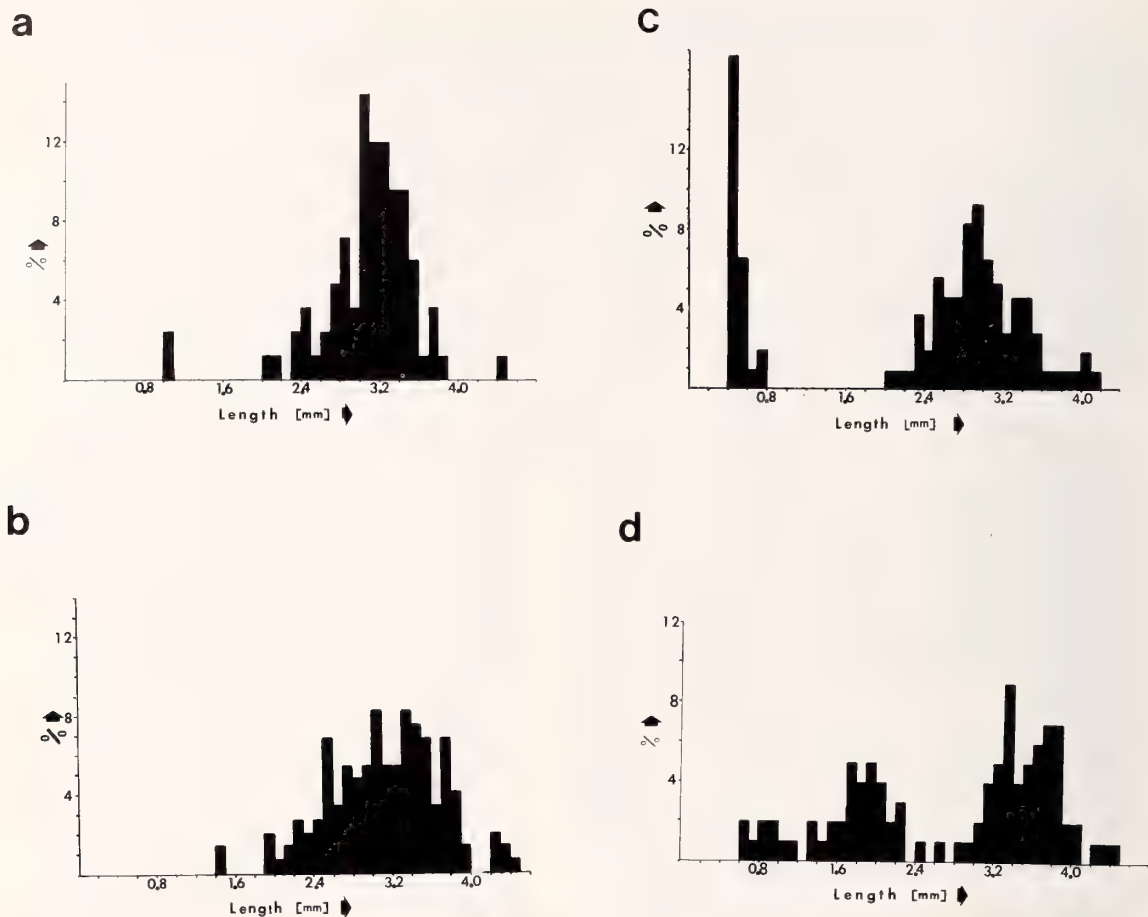


Figure 14

Size-frequency distributions from pooled monthly samples of *Scintillona bellerophon* spec. nov. at Woodward Point. A. October, November, and January 1982 ($n = 147$); B. January, February, and March 1983 ($n = 84$); C. April and June 1983 ($n = 108$); D. September 1983 ($n = 99$).

laboratory-raised juveniles did not attach to their synaptid host (CHANLEY & CHANLEY, 1970).

Ecology

The sediment at Woodward Point is a coarse silt (McDERMID, 1983) and has a prominent algal cover of *Ulva* in summer months. A narrow spit projects across the mouth of Sooke Harbour (Figure 1), and protects the study site from direct wave action (McDERMID, 1983). Specimens of *Leptosynapta clarki* were present from mid to low tide levels, and, in November 1982, occurred in a mean density of 78/0.1 m² (estimated from 13 randomly taken 5.5-cm diameter cores). The holothuroids were found to a depth of 8–10 cm in the sediment, and occupied semi-permanent burrows as they moved slowly through the substratum. In September 1983, 57% of the *Leptosynapta* recovered ($n = 68$) had ≥ 1 attached *Scintillona bellerophon*. The mean number of bivalves per host was $1.69 \pm$

1.05 SE ($n = 39$), and the maximum occurrence on a single holothuroid was 6. Typically *S. bellerophon* attached to the anterior half of *Leptosynapta* in a forward-facing orientation. Adhesion was achieved either by fine byssal threads, or more loosely by the lateral apposition of the extended foot to the integument of the host.

In aquaria, bivalves removed from their hosts usually reattached to any available *Leptosynapta*. Specimens of *Scintillona bellerophon* placed in aquaria without holothuroids remained at the surface or burrowed superficially in the sediment (mean depth = 4 mm \pm 0.2 SE, $n = 10$). Upon the introduction of *Leptosynapta* and subsequent attachment, individuals of *S. bellerophon* were found at significantly greater depths ($\bar{x} = 18$ mm \pm 6 SE, $n = 8$, $P < 0.001$), probably as a result of the holothuroid's burrowing activity. The burrowing and ventilating activities of the holothuroids increased the depth of the lighter colored (oxygenated) sediment zone from 2–3 mm to 45–50 mm.

Three other invertebrate species were frequently found in *Leptosynapta clarki* burrows. Two were polychaetes, *Harmathoe lunulata* (delle Chiaje) and *Pholoe minuta* (Fabricius, 1780); the third was another galeommatacean bivalve, *Mysella tumida* (Carpenter, 1864). Both polychaetes were free in the burrow and tended to cling to the host holothurian. *Mysella tumida* was never seen to attach to the host, but occurred in the oxidized sediment layer immediately surrounding the burrow.

Some of the larger individuals of *Scintillona bellerophon* exhibited 3 growth-arrest rings on their valves, indicating that they may live up to 3–4 years of age. The first growth-arrest ring is formed at a valve length of 1.8–2.6 mm, the size attained by the first year class (Y_0) by their first winter (Figure 14). In 1983, settlement commenced in April, peaked in June, and continued at a reduced rate throughout the summer (Figure 14). By September, individuals recruited in April/June had grown by approximately 1.3 mm in length to reach 1.6–2.1 mm. It would appear that they reach sexual maturity the following spring at a length of 2.4–3.0 mm.

Leptosynapta clarki occurs off the Pacific coast of North America from the Queen Charlotte Islands to Pacific Grove, California (BROOKS, 1973). *Scintillona bellerophon* is, to date, known only from Sooke Harbour. Two nearby sites with dense populations of the holothuroid, Bamfield Inlet (Vancouver Island) and False Bay (San Juan Island, Washington State), apparently do not contain this species (A. Gibson, personal observation, and R. D. Burke, personal communication, respectively). In an ecological study carried out on the Sooke population of *Leptosynapta* in 1973, BROOKS (1973) did not encounter any *S. bellerophon*. This implies that the bivalve colonized this site 4–10 years ago and has since built up a considerable population density.

DISCUSSION

Scintillona bellerophon is similar to *S. zelandicus* in both morphology and mode of life. At least three distinct morphological differences, however, exist between the two (based on ODHNER's (1924) and MORTON's (1957) descriptions and the examination of three specimens of *S. zelandicus*); these are sufficient to give *S. bellerophon* a separate species designation. In *S. bellerophon* the (A) umbone is slightly posterior, the anterodorsal margin being as a result higher than the posterodorsal margin (in *S. zelandicus* the umbone is slightly anterior (personal observation) and the posterodorsal margin is higher), (B) mid-mantle fold is extended posterodorsally into three retractable flaps on either side (not extended in *S. zelandicus*), (C) distal part of the foot contains numerous and prominent longitudinal ciliated grooves (present in reduced form in *S. zelandicus*).

Of the four species found with *Leptosynapta clarki*, *Scintillona bellerophon* is probably the most intimately associated. To the other species, the burrow may only serve

as a temporary refuge or feeding site. *Pholoe minuta* was frequently found outside the burrows, and *Mysella tumida* also occurs as an ectocommensal of the polychaete *Mesochaetopterus taylori* (Ó Foighil, personal observations). *Harmathoe lunulata* has previously been recorded in association with *L. clarki* (BROOKS, 1973) and, in the North Atlantic, with *L. inharens* (O. Fr. Müller) (MORTENSEN, 1927). This is the first record of *P. minuta* and *M. tumida* living as commensals. The ventilating activities of *Leptosynapta* enable these polychaetes and the small, practically siphonless bivalves to live at depth in the substratum by positioning in or around the burrow. This may result in reduced predation pressure (OCKELMANN & MUUS, 1978). *Leptosynapta clarki* does not seem to benefit from the association in any obvious manner.

As well as showing a trend toward commensalism, the members of the Galeommatacea demonstrate various degrees of shell reduction, mid-mantle fold hypertrophy, and reproductive complexity (MORTON, 1976). When *Scintillona bellerophon* and *S. zelandicus* are compared in these respects with other galeommatacean bivalves ectocommensal with synaptid holothurians, they are found to be relatively unspecialized. In *Devonia perrieri* (Malard, 1903), which occurs on *Leptosynapta inharens*, the valves are much reduced, hinge dentition is absent, and the mid-mantle fold extends to almost completely cover the shell surface (ANTHONY, 1916). *Montacuta percompressa*, which also occurs on *L. inharens* (BATESON, 1923), shows secondarily developed sexual dimorphism, in which parasitic, shell-less males occur within the mantle cavity of the female (JENNER & MCCRARY, 1968). This hints that, in evolutionary terms, both *S. bellerophon* and *S. zelandicus* are relative newcomers to this particular ecological niche.

For all ectocommensals, adhesion to the host is obviously important. *Scintillona bellerophon* and *S. zelandicus* achieve this by two means, apposition of the laterally compressed foot and ventral attachment by byssus. In the other bivalves ectocommensal on synaptids, foot morphology varies from the relatively unspecialized condition in *Devonia oskimai* (KAWAHARA, 1942) to that of *D. perrieri*. In the latter species, the foot is dorsoventrally compressed and acts as a sucker when attached to the host, *Leptosynapta inharens*. The byssal gland opens ventrally, and the animal may attach by byssus or by foot adhesion (ANTHONY, 1916; POPHAM, 1940). This would seem to be a more efficient situation than that found in *S. bellerophon* and, presumably, in *S. zelandicus*, because changing from foot to byssal adhesion does not involve a re-orientation of the foot. In *S. bellerophon*, contact depends on the relatively narrow, ventral surface until byssal attachment is achieved.

Synaptid holothurians, in common with many other burrow-constructing benthic invertebrates, create micro-environments in sediments that are colonized by a variety of associated species. Several galeommatacean bivalves have been found occurring ectocommensally on synaptid holothurians (BOSS, 1965). In the northeastern Pacific, *Scin-*

tillona bellerophon is the representative ectocommensal species, exploiting the ecological niche available in *Leptosynapta clarki* burrows.

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A New Species of Leptonacean Bivalve from off Northwestern Peru (Heterodonta: Veneroida: Lasaeidae)

by

JOSEPH ROSEWATER

Department of Invertebrate Zoology, National Museum of Natural History,
Washington, D.C. 20560

Abstract. A new species of leptonacean bivalve, *Pseudopythina muris*, has been found in the respiratory cavity of a polychaete, *Aphrodita*, from off northwestern Peru (R/V *Anton Bruun* SEPBOP cruise 16, sta. 625a; cruise 18B, sta. 764). Mature clams are strongly crescent-shaped and are attached by fine byssal threads to elytra of *Aphrodita*. Young stages are moderately equilateral, but show progressive changes in shape until the adult inequilateral condition is achieved. Characteristics of shell and soft part morphology indicate placement of this species in the superfamily Leptonacea, family Lasaeidae. The unusual shape may be an adaptation to life in the respiratory cavity of *Aphrodita*. Examinations of this and other oddly shaped Leptonacea show that some of these anatomical modifications are functional adaptations to the hosts or commensals with which they are associated.

INTRODUCTION

THE R/V *Anton Bruun* carried out nine cruises during the International Indian Ocean Expedition (IIOE, 1963-1964). In 1965, upon returning to the western hemisphere (cruise 10), the *Anton Bruun* began the Southeastern Pacific Biological Oceanographic Program (SEPBOP, 1965-1966), during which eight cruises were undertaken (cruises 11-18, the last consisting of parts A and B). During cruises 16 and 18B, trawls were made in 90-133 m, off northwestern Peru. Invertebrates captured were forwarded to the Smithsonian Institution's Oceanographic Sorting Center, Washington, D.C., where they were sorted and initial identifications were made. Scale worms, Aphroditidae, are normally sent to M. H. Pettibone, National Museum of Natural History, for study. However, since small bivalves were found clinging to ventral surfaces of some specimens, they were sent first to me. The small bivalves were noted externally and, in addition, upon palpation, hard bodies were felt in the normally soft scale worms. The worms were X-rayed revealing the crescent-shaped clams visible in Figure 1A-F. I dissected the scale worms (*Aphrodita japonica* Marenzeller, 1879) revealing a number of the bivalves, ranging from tiny rather normally shaped specimens, as small as 1 mm in length, to larger crescent-shaped individuals, 10.9 mm in length. Comparison with collections and the literature revealed no known species exhibiting the characteristics of the bi-

valves found in the respiratory cavity of *Aphrodita* (see ROSEWATER, 1983). They are herein described as a new species belonging to the family Lasaeidae.

BOSS (1965) reviewed the commensal relationships of the "Erycinacea" (now Leptonacea; see CHAVAN, 1969, and BOSS, 1982; also see Acknowledgments, herein) and, in an addendum to his paper, mentioned that PONDER (1965) had described the New Zealand leptonacean bivalve *Arthritica hulmei* attached to the elytra of *Aphrodita*, a relationship apparently very similar to the one reported here. Both PETTIBONE (1953) and NARCHI (1969) described the relationship of the east Pacific leptonacean bivalve species *Pseudopythina rugifera* (Carpenter, 1864) with *Aphrodita japonica*, the same worm host involved in the present study. The former was said by Pettibone to occur in the respiratory cavity of the worm, and both Pettibone and Narchi report it to attach externally. It is also known to attach to the crustacean *Upogebia*.

The new species is reminiscent of another crescent-shaped bivalve, *Curvemysella paula* (Adams, 1856), from the Indo-Pacific, although the two differ in details of hinge structure, and in mature stages the new species possesses a more strongly crescent-shaped shell that is equi- or strongly hypertrophied posteriorly, and narrowed anteriorly. Young stages are moderately equilateral, but show progressive changes in shape until the adult inequilateral condition is assumed (see Figure 2).

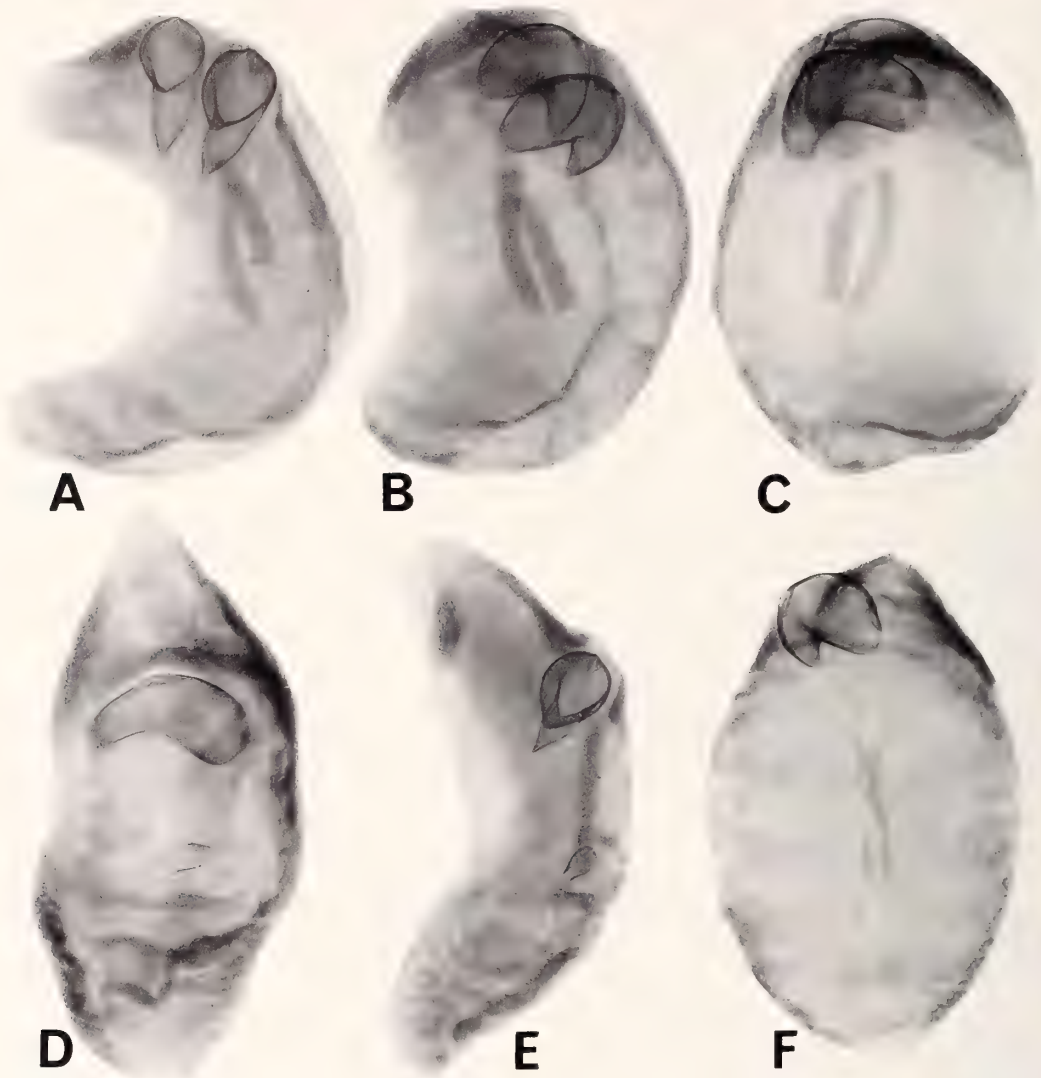


Figure 1

X-rays showing *Pseudopythina muris* spec. nov. *in situ*, in respiratory cavity of *Aphrodita japonica*; larger clams are nearer the posterior end of worm (worms 4–5 cm in length). A–C. Same individual from different angles. D–E. Different individual. F. Another individual. Note in E and F, tiny clams scattered through worm's respiratory cavity.

TAXONOMY

Family Lasaeidae Gray, 1847

GRAY, J. E. 1847:192 [as Lasiadae].

In a recent review of the phylum Mollusca, BOSS (1982) characterized members of the bivalve family Lasaeidae (Subclass Heterodonta: Order Veneroida: Superfamily Leptonacea) as being equivalve, variously shaped, thin, fragile, compressed to more-or-less inflated, umbos submedian, usually less than 20 mm in length, dimyarian, adductors subequal, pallial line simple, hinge variable, antero-posterior respiratory-feeding current, with incur-

rent and excurrent mantle openings located so as to accommodate such a flow. Ctenidia are reduced, limited to inner demibranchs; individuals are monoecious, with evidence of brooding of young in mantle cavity; frequently commensal or parasitic. These features are characteristic of the bivalves found off northwestern Peru in *Aphrodita*, and they are, therefore, included in the Lasaeidae.

Although adult specimens of the new species assume an exaggerated crescent shape, their shells in many ways resemble those of members of only one generic group so far as I have been able to determine, the genus *Pseudopythina* Fischer, 1878. They share a number of similarities with

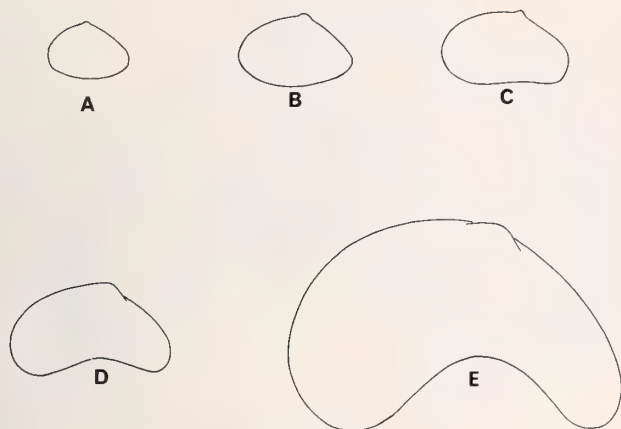


Figure 2

A-E show changes in outline of *Pseudopythina muris* spec. nov. shells from equilateral to inequilateral as growth progresses.

species assigned to that group, including a tendency to associate with *Aphrodita* and certain crustaceans.

Pseudopythina Fischer, 1878

Pseudopythina FISCHER, 1878:178; type species by monotypy, *Kellia macandrewi* FISCHER, 1867:194.

Pseudopythina LOCARD, 1892:317 [invalid emendation for *Pseudopythina* Fischer, 1878]; LOCARD, 1898:303.

The type species, *Kellia macandrewi* Fischer, is an inhabitant of southern European seas. Its characteristics were pointed out by CHAVAN (1969) in his description of *Pseudopythina*: "transverse trigonal, very inequilateral, anteriorly attenuated and elongate; enlarged and rounded backward [posteriorly], smooth." Hinge teeth are simple and consist of a single curved, projecting cardinal tooth in either valve, just beneath the umbos, posterior to which is located a well developed, and mostly internal ligament. The other cardinals and anterior and posterior lateral teeth are much reduced and limited to weak thickenings of the dorsal valve margins. Cardinal teeth of the type species, *P. macandrewi*, are more heavily developed than in other species examined, and may be supported by basal thickening. The anterior adductor muscle scar is usually elongate, the posterior more rounded. A pallial line is evident in some species, usually well inset from shell margins. Externally, shells are smooth with a thin, often wrinkled periostracum, which may be reflected onto the interior edge of the shell. Faint radiating rays are present and are most noticeable at the ventral margin. Shells often show a ventral embayment developed variously in different species; strongest in the new species described herein. *Pseudopythina compressa* DALL, 1899, shows little evidence of such an embayment, prompting DALL (1899) to suggest its normal form results from the lack of a commensal relationship, although OLDROYD (1924) stated that all *Pseudopythina* are commensals.

The anatomy of *Pseudopythina* was described and il-

lustrated by NARCHI (1969) in his study of the species *P. rugifera* (Carpenter, 1864) and verified by me through examination of the new species from off Peru. I disagree with the transfer by ABBOTT (1974) of the West Coast species previously assigned to *Pseudopythina* Fischer to *Orobitella* DALL, 1900. The characteristics of *Pseudopythina macandrewi* are quite different from those of the type species of *Orobitella*, *O. floridana* DALL, 1899, with its regular and often deeply incised concentric sculpture, large rounded to squarish adductor muscle scars, posteriorly displaced umbos, and pellucid shell, or from the similar appearing *Neaeromya* Gabb, 1873 (type species, *N. quadrata* Gabb, 1873), with which both ABBOTT (1974) and BERNARD (1983) ally *Orobitella*.

There are representatives of *Pseudopythina* in the several marine faunal regions with the exception of the west Atlantic. An abbreviated catalogue of the Recent species follows. Until the anatomy of each species is studied and compared, however, it will not be possible to state with certainty whether or not these species are really related.

East Atlantic

Pseudopythina macandrewi (FISCHER, 1867):194 (Nord de l'Espagne; bassin d'Arcachon (Gironde) [Bay of Biscay, France]); not in Journal de Conchyliologie Type Collection (FISCHER-PIETTE, 1950); may be in British Museum (NH) (DANCE, 1966); syntypes (?) ex MacAndrew in Jeffreys Collection, USNM 170637, from Vigo Bay, Spain.

Remarks—This is the type species of *Pseudopythina* Fischer, 1878. It is listed as a junior synonym of *P. setosa* (Dunker, 1864) by JEFFREYS (1881), LOCARD (1898), CHAVAN (1969), NORDSIECK (1969), and QUILS (1973). The last four authors seem to have ignored the statement by JEFFREYS (1882) that Dunker's species is the young of *Corallophaga lithophagella* (Lamarck, 1819), a member of the Trapeziidae (see LAMY, 1920:283). The name specified by JEFFREYS (1882) as having priority over *P. macandrewi*, *Sportella caillati* Conti, 1864, attributed by the latter to "Deshayes, 1852," apparently is a manuscript name. The name was validly introduced by DESHAYES (1860:596) for an unrelated fossil. So far as I can determine, Fischer's name, *Kellia macandrewi*, is the oldest valid taxon for this entity.

Other east Atlantic species assigned to *Pseudopythina* are:

Pseudopythina geoffroyi geoffroyi (Payraudeau, 1826), NORDSIECK (1969:90)

Pseudopythina geoffroyi complanata (Philippi, 1836), NORDSIECK (1969:90).

Remarks—I have been able to find no information on commensalism in these species.

East Pacific

Of the several east Pacific species included in *Orobitella* DALL, 1900, by ABBOTT (1974), the only three that seem

to be referable to *Pseudopythina* are listed below. The remainder probably belong in *Orobitella* or other groups. Their ultimate placement will depend on analysis of anatomical relationships impossible at this time.

Pseudopythina rugifera (CARPENTER, 1864):602, 643 (Puget Sound; syntypes USNM 4445); CARPENTER, 1865: 57.

Remarks—Although this species is dated from Carpenter, 1864, without a prior concept it is difficult to recognize without reference to the type specimens. His 1865 description is much more complete. NARCHI (1969), who has made the most intensive studies on this species to date, discussed its anatomy thoroughly and also its commensal relationships with the crustacean *Upogebia* and the polychaete *Aphrodita*. The species is very similar in its general appearance to the new species being described herein, although lacking the extreme crescent shape. The species *P. rugifera* is distributed from Alaska to Baja California, Mexico, according to ABBOTT (1974). The following are synonyms of *P. rugifera* according to BERNARD (1983:32): *Lepton rude* Whiteaves, 1880, *Sportella californica* Dall, 1899, and *Pseudopythina myaciformis* Dall, 1916.

Pseudopythina stearnsii (DALL, 1899):879, 885 (Gulf of California; holotype USNM 73701). BERNARD, 1983:32.

Remarks—*Sportella stearnsii* Dall, 1899, is placed by BERNARD (1983, as *Neaeromya*) close to *P. rugifera* and *P. compressa*. The unique holotype has a much heavier shell and cardinal teeth than the other West Coast species, more reminiscent of the type species, *Pseudopythina macandrewi* (Fischer, 1867).

Pseudopythina compressa DALL, 1899:880, 888 (south of Nunivak Island [SW of Hagemester Island, USFC sta. 3305], Alaska; holotype USNM 107855).

Remarks—This species is less inflated and has a more rounded outline than *P. rugifera*, but has the characteristic single cardinal tooth and ligament of *Pseudopythina*. DALL (1899) pointed out that, due to its uniform shape, it probably is not a commensal species. Most distributional records for this species are from northern waters, Alaska, north of the Aleutian Islands, south to British Columbia, in from 10 to 150 m (BERNARD, 1983). The record mentioned by ABBOTT (1974), off Acapulco, is based on USNM 210171, USFC station 3422, in 258 m, a typical specimen. The species is listed by HABE (1977) as a *Squillaconcha*, (see below).

Indo-Pacific

Subgenus *Squillaconcha* KURODA & HABE, 1971:627, 404; type species by original designation: *Kellia subsinuata* Lischke, 1871.

Remarks—This taxon was proposed at subgeneric rank to contain Japanese species formerly assigned to *Pseudopythina*. Its justification seems to be based mainly on the geographical and host differences.

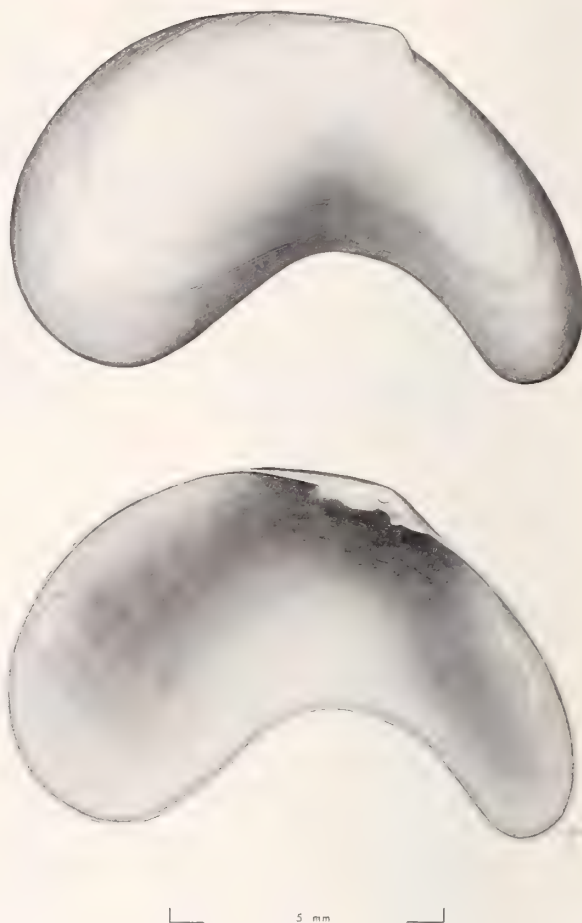


Figure 3

Shell of *Pseudopythina muris* spec. nov. Upper figure: exterior. Lower figure: interior of shell showing anterior (right) and posterior adductor muscle scars and characteristics of the hinge.

Pseudopythina (Squillaconcha) subsinuata (LISCHKE, 1871):43 (Japan; type in Academy of Sciences, Leningrad).

Remarks—This species often is found as a commensal on mantis shrimps. It is distributed in Japan on the islands of Honshu, Shikoku, and Kyushu. According to HABE (1964) it incubates its larvae in the branchial chamber.

Pseudopythina (Squillaconcha) sagamiensis HABE, 1961: 151 (Zushi City, Kanagawa Prefecture, Japan; type in National Science Museum, Tokyo).

Remarks—*Pseudopythina sagamiensis* was added to *Squillaconcha* by HABE (1977), who also included *P. compressa* Dall, 1899, which is here referred to *Pseudopythina* sensu stricto. *Pseudopythina sagamiensis* is said to differ from *P. subsinuata* in being more narrowly elongate and smaller in size than the former. Its commensal relationships apparently are unknown.

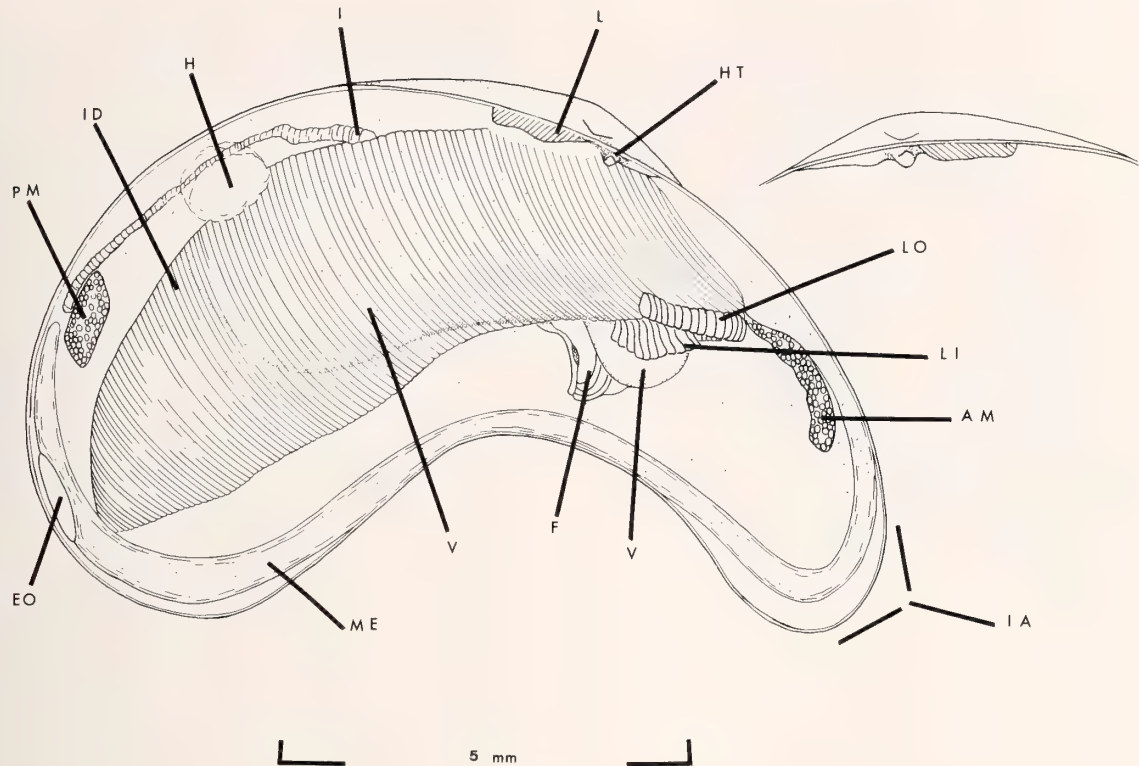


Figure 4

Anatomy of *Pseudopythina muris* spec. nov. and detail of hinge of right shell valve (see Abbreviations listed at end of text).

Pseudopythina muris Rosewater,
spec. nov.

(Figures 3, 4; Table 1)

Description: Shell reaching 10.9 mm in length; mature individuals have a crescent-shaped outline; valves inflated posteriorly and narrowed anteriorly. Valves thin and translucent, but not excessively fragile; color gray externally where not covered with thin, light-yellow periostracum; internally valves smooth, porcelainous, and shining. External surface smooth. Radial sculpture of fine threads originating at umbos and radiating anteriorly, posteriorly, and ventrally to shell margins. Threads visible from internal surface by transmitted light. Concentric sculpture consisting of well-marked lines of growth accentuated by areas of crowding which outline transition in shell shape from only moderately to strongly inequilateral. Dorsal margin broadly convex in mature individuals; ventral margin markedly concave. Distance from umbos to posterior margin exceeds distance from umbos to anterior margin. Shell posteriorly hypertrophied, possibly for brooding. Hinge teeth consist of single small, protruding, peg-like cardinal in each valve which interdigitates with its counterpart just anterior to internal opisthodetic ligament that helps join valves. Dorsal margin thickened for

considerable distance both anterior and posterior to umbos. Umbos directed antero-medially. Pallial line not evident. Anterior adductor muscle scar hardly visible, long and narrow as interpreted from animal's anterior muscle; posterior adductor muscle scar less elongate than anterior scar. Prodissoconch small (about 30 μ m in length) fan-shaped, shining.

Animal with thickened mantle edge; mantle open antero-ventrally forming incurrent-pedal aperture area. Well-marked excurrent aperture located posteriorly. Mantle open from ventral border of excurrent aperture to region of lower border of anterior adductor muscle scar. Ctenidium consists of only single demibranch, probably the inner, but there appear to be both inner and outer labial palps. Foot small, with well-marked byssal groove.

Holotype: USNM 836636; from R/V *Anton Bruun* SEP-BOP Cruise 18B, Station 764; Lat. 4°06'S; Long. 81°09'W; off NW Peru; 90 m; 8 September 1966; length 10.7 mm; height 6.6 mm.

Paratypes: 51 paratypes USNM 836637; from same station; ranging in length from 1 to 10.9 mm; height from 0.8 to 7.4 mm.

Other specimens: 4 specimens USNM 836638; from R/

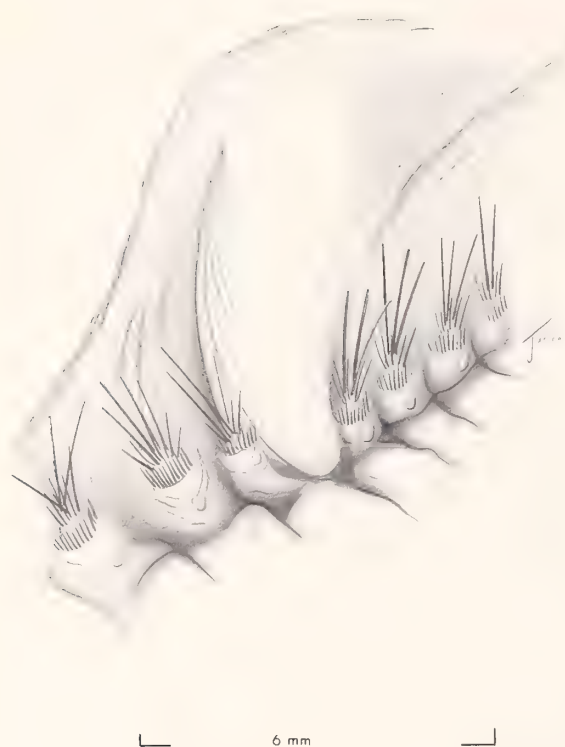


Figure 5

Detail showing anterior end of a *Pseudopythina muris* spec. nov. protruding from between parapodia of *Aphrodita japonica*.

V Anton Bruun SEPBOP Cruise 16, Station 625a; Lat. 4°57'S to 5°01'S; Long. 81°23'W; off NW Peru; 118–133 m; 2 June 1966; ranging in length from 2.6 to 5.1 mm; height from 1.8 to 2.7 mm.

Etymology: *muris*—genitive singular of the feminine (or masculine) Latin substantive noun *mus* (mouse), meaning “of the mouse,” alluding to the presence of *Pseudopythina muris* spec. nov. in the respiratory cavity of the seamouse *Aphrodita japonica* Marenzeller, 1879.

Remarks: *Pseudopythina muris* spec. nov. was found in the respiratory cavity of *Aphrodita japonica* at two R/V Anton Bruun stations in 90–133 m, from off northwestern Peru in June and September 1966. The fact that at least 52 bivalves were found in 7 worms from one of the stations indicates that this probably is not an adventitious relationship, although the other bivalve living with *Aphrodita* in the east Pacific, *Pseudopythina rugifera*, also inhabits a crustacean. In some cases, commensal relationships may be purely fortuitous and based on the availability of a suitable substratum, which happens to be another animal. In this case the clam appears to be at least partially adapted to the *Aphrodita* host. The first individuals noticed were attached by byssal threads to the ventral surfaces of the *Aphrodita* in the vicinity of the parapodia. Those discovered within the respiratory chamber of the worms were byssally attached to the surfaces of the worms' elytra, and on at least two occasions, mature *Pseudopythina muris* were found with their anterior ends protruding from between two parapodia outside a worm's respiratory chamber

Table 1

Measurements of *Pseudopythina muris* spec. nov. from R/V Anton Bruun SEPBOP Cruises 16, Station 625a, and 18B, Station 764 (N = number of individuals in sample; M = arithmetic mean; SD = standard deviation; V = variance; H/L = ratio of shell height to length produced by dividing height by length).

	Station 764							Summary	
	Clams in worm 1	Clams in worm 2	Clams in worm 3	Clams in worm 4	Clams in worm 5	Clams in worm 6	Clams in worm 7	Station 764	Station 625a
N	21	6	6	5	5	5	4	52	4
Length (mm)									
Range	1.0–10.7	1.8–9.6	1.4–10.7	1.4–10.9	1.6–10.7	2.1–3.2	1.8–4.8	1.0–10.9	2.6–5.1
M	2.20	3.40	3.13	5.36	3.88	2.44	3.45	3.03	3.75
SD	1.94	2.80	3.39	4.25	3.44	0.42	1.25	2.77	0.89
V	3.75	7.84	11.48	18.08	11.81	0.18	1.55	7.69	0.79
Height (mm)									
Range	0.8–6.4	1.3–6.4	1.0–6.9	1.1–7.4	1.0–6.6	1.4–2.1	1.3–2.4	0.8–7.4	1.8–2.7
M	1.50	2.20	2.13	3.64	2.36	1.58	1.93	1.99	2.18
SD	1.12	1.87	2.14	2.87	2.14	0.27	0.42	1.76	0.33
V	1.25	3.48	4.56	8.25	4.57	0.74	0.18	3.08	0.11
H/L									
Range	0.60–0.80	0.62–0.72	0.65–0.79	0.64–0.79	0.39–0.72	0.62–0.67	0.49–0.72	0.39–0.80	0.53–0.69
M	0.71	0.67	0.72	0.69	0.62	0.65	0.60	0.68	0.59
SD	0.05	0.03	0.04	0.05	0.12	0.02	0.10	0.07	0.06
V	0.002	0.001	0.002	0.003	0.141	0.0004	0.010	0.005	0.107

(Figure 5). It is assumed this situation would provide the clam with a direct source of fresh seawater for feeding and respiration while the clam's posterior portion is well protected inside the worm's respiratory cavity.

Although the clams have not been sectioned to determine their sexuality, leptonaceans are known to be mon-ocious, and this mode of reproduction certainly would be advantageous to an animal that may be isolated in a worm's respiratory cavity. How clams travel between hosts is unknown. Leptonaceans are known to walk, however, and young may be drawn into a worm's respiratory cavity through its incurrent points. Frequently there is a range of individuals present in a worm, from smallest to largest sizes (Table 1). Usually there is only a single large individual, but, in two cases, two large individuals were present in a worm. The other clams present are mostly of smaller sizes: 1–5.1 mm in length. It is strongly suspected that these young are produced ovoviviparously via a brood pouch occupying the hypertrophied, globose posterior ends of the larger specimens (see Figure 1, showing X-rays taken from different angles to reveal expanded nature of shells). An example of the pattern of distribution of different sized clams in a worm is shown in the drawing (Figure 6).

In the adult stage, *Pseudopythina muris* is easily distinguished from the other West Coast *Pseudopythina* due to its exaggerated crescent shape and hypertrophied posterior. The other species are oval to subrhomboidal in outline, although there is clear evidence of an embayment in the ventral margin of *P. rugifera* (see discussion under *Pseudopythina*). *Pythinella sublaevis* (CARPENTER, 1857: 112) frequently has shell curvature, but it differs from *Pseudopythina* in hinge morphology and is unrelated.

The unusual shape of *Pseudopythina muris* may be an adaptation to life in the respiratory cavity of *Aphrodita*. The oddly shaped shells of other Leptonacea provide evidence of functional adaptations. *Curvemysella paula* lives in association with a hermit crab (HABE, 1959). Similarly, bivalves such as *Rochefortia* and *Pythinella*, with curved ventral margins, nestle in apertures and boreholes of gastropod shells where the curvature provides a secure purchase (personal observations). The shell of *Aligena cokeri* Dall, 1909, is grooved from near the umbos to its ventral margin, reflecting a mid-ventral byssal attachment to the tube of the Panamic polychaete *Mesochaetopterus alipes* Monro, 1928 (also see MONRO, 1933, and ROSEWATER, 1976). When the mode of life of these and other aberrant-looking bivalves is understood, there is often a functional explanation for their peculiar appearances.

Further testimony to the major change in shape undergone during the maturation of *Pseudopythina muris* may be noted in the table of measurements. There is an especially wide range in the ratio of height to length: 0.39–0.80. This indicates the transition from rather elongate young (0.39) to the mature individuals whose strong crescent shape causes the more nearly 1:1 ratio of height to length.

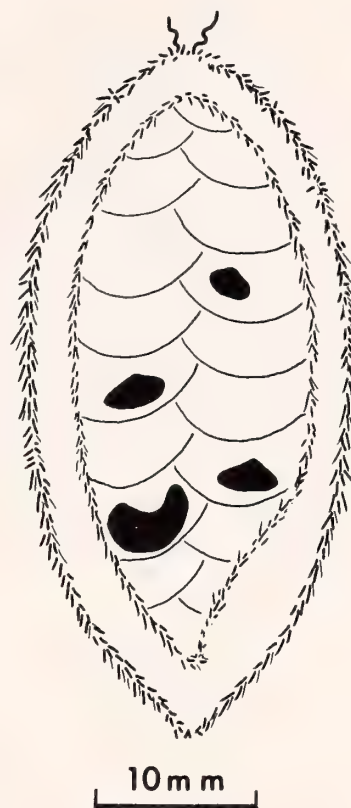


Figure 6

Various growth stages of *Pseudopythina muris* spec. nov. *in situ*, attached to elytra of *Aphrodita japonica* (dorsal covering of respiratory cavity, or "burlap," is cut away).

ABBREVIATIONS

The following institutional, program, and anatomical abbreviations are used in this paper.

AM	anterior adductor muscle
ANSP	Academy of Natural Sciences of Philadelphia
CAS	California Academy of Sciences
eo	excurrent opening
f	foot
h	heart
ht	hinge tooth
i	intestine
ia	incurrent area
id	inner demibranch
l	ligament
li	inner labial palp
lo	outer labial palp
MCZ	Museum of Comparative Zoology, Harvard University
me	mantle edge
NMNH	National Museum of Natural History, Smithsonian Institution
pm	posterior adductor muscle

SEPBOP South Eastern Pacific Biological Oceanographic Program
 USNM United States National Museum (NMNH)
 v visceral mass

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Two anonymous reviewers made helpful recommendations among which was the suggestion that I use the superfamily name Galeommatacea in place of Leptonacea, based on date priority. The latter is not a current requirement of the ICZN for names above family level, nor do I consider it a productive procedure in groups such as Leptonacea that are in a state of flux as concerns our understanding of biological and nomenclatorial entities. For those who wish to follow strict date priority to class level in the Bivalvia, BERNARD (1983) includes a great deal of useful and detailed information.

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Vitrea contracta (Westerlund) and Other Introduced Land Mollusks in Lynnwood, Washington

by

BARRY ROTH

California Academy of Sciences, San Francisco, California 94118

AND

TIMOTHY A. PEARCE

Department of Paleontology, University of California,
Berkeley, California 94720

Abstract. The introduced land mollusk species *Vitrea contracta* (Westerlund, 1871), *Cionella lubrica* (Müller, 1774), *Oxychilus alliarius* (Miller, 1822), *Arion rufus* (Linnaeus, 1758), *Arion subfuscus* (Draparnaud, 1805), *Limax maximus* Linnaeus, 1758, and *Deroceras reticulatum* (Müller, 1774) occur in Lynnwood, a suburb of Seattle, Washington. All are natives of Europe and introduced and dispersed through human agency, probably including the use of leaves from other lots as mulch.

THE ONLY previous records of the European zonitid land snail *Vitrea* (*Crystallus*) *contracta* (Westerlund, 1871) in North America are from the San Francisco Bay area, California (ROTH, 1977). There it was found in leaf litter and on stems of ivy in landscaped or otherwise disturbed areas of San Francisco, and in drift taken from around Lake Merritt, Oakland.

In August 1983, we found *Vitrea contracta* in Lynnwood, a suburb of Seattle, Washington. The occurrence is in two adjacent groves of red alders (*Alnus rubra*), each about 10 × 10 m in dimension, planted as woodlots on property between 44th Avenue W. to the east, 188th Street S.W. to the south, 46th Avenue W. on the west, and an unnamed driveway to the north (SE¼ NE¼ sec. 16, T. 27 N, R. 4 E, Willamette Base and Meridian; USGS Edmonds East Quadrangle [7.5-minute series, topographic], ed. 1953, photorev. 1981).

The ground is well drained and carpeted by a loose cover of creeping buttercup (*Ranunculus repens*). At this time of the year few other herbs were apparent. Under the buttercup was about 2-4 cm depth of leafmold, consisting mainly of leaves of the alders and bigleaf maple (*Acer macrophyllum*) from a large tree growing within a few meters of the alder groves.

According to the owners, the alders were planted in 1978. They were brought in as first- or second-year seedlings, purchased from a nursery in Bothell, Washington. The groves and adjoining grounds have been mulched since

1975 with cow manure from a dairy in Bothell and with leaves and grass clippings from parks and other properties within a 24-km radius, some areas as far away as Seattle. Before its use as a woodlot, the area now occupied by the groves was used to grow strawberries. The carrying in of leaves for mulch provides an obvious avenue of introduction for litter-dwelling mollusks.

Both living snails and empty shells of *Vitrea contracta* were moderately common. The largest specimen found is an empty shell 2.35 mm in diameter with 4.4 whorls. The smallest, a live-collected individual, is 0.66 mm in diameter with 2.0 whorls.

In the Old World, *Vitrea contracta* is widespread in the British Isles as far north as the Outer Hebrides and extends throughout France, Germany, and the Low Countries. It occurs in Iceland but is absent from much of central and northern Scandinavia (ROTH, 1977; KERNEY & CAMERON, 1979). In the U.S.S.R. it occurs in the Baltic region, the Vitebsk region, and the western regions of the Ukraine (LIKHAREV & RAMMELMEIER, 1952). FORCART (1973) reported it from Palestine. KUIPER (1964) and EVANS (1972) have published habitat notes.

Other introduced land mollusks associated with *Vitrea contracta* at this site are *Cionella lubrica* (Müller, 1774), *Oxychilus alliarius* (Miller, 1822), *Arion rufus* (Linnaeus, 1758), and *Arion subfuscus* (Draparnaud, 1805). The first two species are common at the site. *Arion rufus* and *A. subfuscus* are not common in the alder groves but are more

numerous around flower pots, wood on the ground, and stacked construction blocks nearby. *Deroceras reticulatum* (Müller, 1774) was not found in the groves but occurs within 20 m, under potted plants. *Limax maximus* Linnaeus, 1758, was not found at the site in August 1983 but was collected earlier, in July 1980. In November 1979 it was found in a greenhouse on the same property.

Cionella lubrica has not been reported previously from the Puget Sound valley. The only other Washington record is from Walla Walla (PILSBRY, 1948). This Holarctic species occurs naturally in North America, as shown by its presence in deposits of Yarmouthian age in the Great Plains (LEONARD, 1950). However, it is decidedly synanthropic, and its occurrences in settled areas such as the suburbs of Seattle likely involve transport by humans.

The American distribution of *Oxychilus alliarius* is very incompletely known, partly because of the difficulty some authors have had distinguishing among the several introduced species of *Oxychilus* (cf. HANNA, 1966). Records from Victoria, British Columbia (LA ROCQUE, 1953), and Newport, Oregon (HANNA, 1966), place *O. alliarius* in the Pacific Northwest, but it has not been reported previously from the Seattle area. KOZLOFF (1976) indicated that *O. alliarius* is the most common *Oxychilus* in backyards in the Pacific Northwest, but did not cite specific localities. Its native range includes northern and western Europe and Iceland (KERNEY & CAMERON, 1979). The present specimens were identified while alive by their garlic-like aroma and by comparison of the shells with the excellent diagnosis and illustrations of KERNEY & CAMERON (1979).

Arion rufus was identified by comparing the reproductive system with the figures and diagnoses of CAIN & WILLIAMSON (1959), QUICK (1947, 1960), and KERNEY & CAMERON (1979). Diagnostic features include the large, bulky, upper atrium and a vas deferens 1.5–2 times as long as the epiphallus. *Arion ater* (Linnaeus, 1758) and *A. rufus* are regarded by some authors as separate species (QUICK, 1947; WALDÉN, 1976) and by others as subspecies (CAIN & WILLIAMSON, 1959; QUICK, 1960; ROLLO & WELLINGTON, 1975; KERNEY & CAMERON, 1979). CAIN & WILLIAMSON (1959), although presenting evidence that the relationship is subspecific, regarded the taxonomic status as unsettled (p. 82). WALDÉN (1976) remarked that the evidence was not conclusive; we follow him in treating *A. rufus* as a species. We believe that more restrictive criteria must be met to recognize a subspecies than a species; therefore, when the evidence is inconclusive, the conservative approach is to treat the taxon in question as a species.

R. T. Paine (reported by GETZ & CHICHESTER, 1971) believed *A. ater* to be restricted to more rural areas in the Pacific Northwest, while *A. rufus* was more or less confined to cities. The criteria he used to recognize the two taxa were not specified. ROLLO & WELLINGTON (1975) summarized the history of accounts of "*Arion ater*" (including *A. rufus*) in the Pacific Northwest. They reported that dissected specimens from the vicinity of Vancouver

had genitalia more like *rufus* than *ater* as described by QUICK (1947) and noted that a figure of an Oregon specimen by PILSBRY (1948) also appeared to be *rufus*.

Arion subfuscus has been reported from the Pacific Northwest previously by GETZ & CHICHESTER (1971) and ROLLO & WELLINGTON (1975). In the vicinity of Vancouver, British Columbia, *A. subfuscus* occurs in both cultivated areas and natural woodland, probably becoming introduced to the woods when gardeners dumped garden refuse and compost in such areas (ROLLO & WELLINGTON, 1975). The native range of *A. subfuscus* includes most of Europe (LIKHAREV & RAMMELMEIER, 1952; KERNEY & CAMERON, 1979); it has also been introduced into northeastern North America (PILSBRY, 1948; CHICHESTER & GETZ, 1969). To our knowledge, this is the first report of the species from the Puget Sound valley. The present specimens were identified by dissection. According to WALDÉN (1976:25), "*A. subfuscus* shows a complicated subspecific taxonomy. It is not excluded that further research will show that an aggregate species is involved."

Limax maximus has long been known as an introduction in the Pacific Northwest (PILSBRY, 1948; HANNA, 1966; GETZ & CHICHESTER, 1971; ROLLO & WELLINGTON, 1975). HANNA (1966) summarized several reports of *Deroceras reticulatum* in western Washington from the pest-control literature. ROLLO & WELLINGTON (1975) found it the most abundant species in British Columbia. Both *L. maximus* and *D. reticulatum* are widespread in temperate Europe and introduced by commerce to North America and elsewhere.

Voucher specimens of these species are on deposit in the California Academy of Sciences. We gratefully acknowledge the support and forbearance of Mr. and Mrs. C. K. Pearce, Jr. of Lynnwood.

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Determining the Area of a Gastropod's Foot¹

by

RONALD V. DIMOCK, JR.

Department of Biology, Wake Forest University,
Winston-Salem, North Carolina 27109

Abstract. A photographic procedure involving the weighing of enlarged images of the foot of the prosobranch *Ilyanassa obsoleta* has been applied to the problem of determining the area of a gastropod's foot. The results have been compared with those derived from a microcomputer-assisted video scanning procedure and with estimates of pedal area employing conventional elliptical and rectangular geometric models of foot shape. Significant differences in the quantitative predictions of regression models of pedal area as a function of snail size occurred among the six techniques used to determine pedal morphometry. The photography-weighing technique was highly reliable and compared favorably with video scanning. The geometric models over- or underestimated pedal surface area differentially as a function of both the size of a snail and the selection of a width parameter for the calculation of geometric area.

INTRODUCTION

For non-pelagic motile gastropods the ventral surface of the foot is important not only for locomotion but also for the maintenance of position against the effects of gravity, wind and waves. A comprehensive understanding of gastropod pedal morphology and locomotory mechanisms might include a description of locomotory types (MILLER, 1974a), an analysis of adaptive and functional attributes (MILLER, 1974b; GAINES, 1976; LINSLEY, 1978; PALMER, 1980), and knowledge of behavioral aspects of locomotion (BRETZ & DIMOCK, 1983; DIMOCK, in press). In such studies it is often important to have an estimate of quantitative parameters of pedal morphology. However, the measurement of fleshy, mucus-secreting morphological features of a motile soft-bodied organism may not always be readily effected.

In this paper I present a photographic approach to quantifying morphometric parameters of the foot of the marine mud snail *Ilyanassa obsoleta* (Say, 1822). The data from this technique are compared with those derived from a microcomputer-based video image analyzer, as well as calculations of conventional geometric models of pedal surface area. The photographic procedure is shown to be highly reliable. It is readily adaptable to conditions (or species?) under which standard geometric models may yield grossly inaccurate estimates of pedal morphometry.

MATERIALS AND METHODS

All specimens of *Ilyanassa obsoleta* were collected from the Newport River marshes near Morehead City, North Car-

olina. The foot of each of 20 animals (shell length = 9.1–18.3 mm) was photographed as a snail crawled vertically up the side of a glass aquarium. Several exposures were made of each animal and also of lined graph paper (5 mm squares) held against the inside of the same wall of the aquarium. All of the exposures were taken at the same distance from the aquarium with a 35-mm camera with close-up lenses. The exposure in which a snail's foot appeared most nearly bilaterally symmetrical was selected for printing.

Three prints of each snail's foot and seven of the graph paper were enlarged (about 6 ×) and processed identically with an automatic print processor. After the prints were dried, each image of a snail's foot was carefully cut from the photographs and weighed to 0.1 mg. The area of the pedal surface was estimated by comparison to the mean weight of a standard "1 cm²" as determined from the prints of the graph paper. The dimensions of a snail's foot were determined by reference to the grid system of the photographs of the graph paper, with foot width being measured both as the maximum width, exclusive of the antero-lateral horns of the propodium, and the width at one-half foot length.

Each cutout image of a snail's foot was also scanned with a microcomputer-based video image analyzer (Darwin Instrument Company, Winston-Salem, NC) which utilizes an analytical video camera with appropriate digitizer to computer interface and associated software to resolve such parameters as the length, width, or area of an image (TELEWSKI *et al.*, 1983). The area of the foot was also calculated as the area of an ellipse and of a rectangle with the two measures of width described above.

The association of logarithm foot area with logarithm shell length was assessed by Pearson's product-moment

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Table 1

The magnitude and accuracy of various estimates of the pedal area of *Ilyanassa obsoleta* in reference to shell length (SL), foot length (FL), and foot width (FW) expressed both as maximum width (A) and width at one-half FL (B).

SL (mm)	FL (mm)	FW (mm)		Estimated area (mm ²)						Difference (as % of “by weight”)				
				By weight	By video	By ellipse		By rectangle		Video	Ellipse		Rectangle	
		A	B			A	B	A	B		A	B	A	B
9.1	7.3	3.6	3.1	20.1	20.0	20.6	17.8	26.3	22.6	−0.5	+2.5	−11.4	+30.8	+12.4
10.2	7.9	4.0	3.3	23.7	23.0	24.8	20.5	31.6	26.1	−3.0	+4.6	−13.5	+33.3	+10.1
10.2	8.4	4.1	3.6	26.5	25.9	27.0	23.8	34.4	30.2	−2.3	+1.9	−10.2	+29.8	+14.0
10.9	9.6	5.3	4.8	40.6	40.8	40.0	36.2	50.9	46.1	+0.5	−1.5	−10.8	+25.4	+13.5
11.0	8.4	4.4	3.8	27.3	26.8	29.0	25.1	37.0	31.9	−1.8	+6.2	−8.1	+35.5	+16.8
12.7	10.3	5.0	4.3	40.8	40.1	40.5	34.8	51.5	44.3	−1.7	−0.7	−14.7	+26.2	+8.6
13.5	11.5	6.1	6.0	58.1	59.4	55.1	54.2	70.2	69.0	+2.2	−5.2	−6.7	+20.8	+18.8
14.2	12.1	6.2	5.6	57.9	57.8	58.9	53.2	75.0	67.8	−0.2	+1.7	−8.1	+29.5	+17.1
14.3	12.9	5.7	5.2	60.0	60.2	57.8	52.7	73.5	67.1	+0.3	−3.7	−12.2	+22.5	+11.8
14.5	12.5	5.5	5.0	54.9	54.4	54.0	49.1	68.8	62.5	−0.9	−1.6	−10.6	+25.3	+13.8
15.1	12.8	6.2	5.6	61.7	62.3	62.3	56.3	79.4	71.7	+1.0	+1.0	−8.8	+28.7	+16.2
15.2	13.7	6.3	5.8	71.5	72.8	67.8	62.4	86.3	79.5	+1.8	−5.2	−12.7	+20.7	+11.2
16.3	12.9	6.5	6.1	67.3	68.8	65.9	61.8	83.9	78.7	+2.2	−2.1	−8.2	+24.7	+16.9
16.4	12.9	6.9	6.8	73.4	74.1	69.9	68.9	89.0	87.7	+1.0	−4.8	−6.1	+21.3	+19.5
16.7	13.1	7.4	7.3	80.1	81.9	76.1	75.1	96.9	95.6	+2.2	−5.0	−6.2	+21.0	+19.4
16.8	15.5	6.7	6.2	84.7	83.3	81.6	75.5	103.9	96.1	−1.7	−3.7	−10.9	+22.7	+13.5
17.3	16.0	7.6	6.9	95.2	95.3	95.5	86.7	121.6	110.4	+0.1	+0.3	−8.9	+27.7	+16.0
17.3	14.0	7.1	6.7	81.5	80.4	78.1	73.7	99.4	93.8	−1.3	−4.2	−9.6	+22.0	+15.1
17.6	16.1	7.0	6.4	88.4	88.2	88.5	80.9	112.7	103.0	−0.2	+0.1	−8.5	+27.5	+16.5
18.3	15.3	7.9	7.4	96.5	96.4	94.9	88.9	120.9	113.2	−0.1	−1.7	−7.9	+25.3	+17.3
X̄ = −0.1										−1.1	−9.7	+26.0	+14.9	

correlation for each of the six measures of foot area. The slopes and elevations of the resulting regression equations were compared by analysis of covariance (ANOCOVA); significant differences among the regressions were resolved with Student-Newman-Keuls multiple range test (SNK; ZAR, 1974).

RESULTS

All weights of a standard cm² of the enlarged photographic prints were within 1.8% of the mean ($n = 7$); no print of a snail's foot varied more than 2.0% from the mean weight ($n = 3$) for that animal.

The morphometric data for 20 specimens of *Ilyanassa obsoleta* are presented in Table 1. The video scan procedure and the weighing technique were virtually identically precise for determining the area of the image of a snail's foot. However, the elliptical and rectangular models consistently over- or underestimated the area of pedal surface relative to the weighing technique (Table 1). When the area of the foot was modeled as an ellipse, both the sign and the magnitude of the error in estimating pedal area were influenced by the way the width of the foot had been determined.

There was no consistent pattern of the error of estimating pedal area with the elliptical model when the area was calculated using the maximum width. However, when

the width was taken as that at one-half of foot length, the error varied with the size of the snail; the coincidence of the elliptical model of pedal area with the area determined by the weighing technique was positively correlated with shell length ($r = 0.449$, $df = 18$, $P = 0.047$). Thus, the area of the foot of a small specimen of *Ilyanassa obsoleta* was less accurately modeled by an ellipse when foot width was measured at one-half foot length (Table 1), but the precision of the elliptical model increased with increasing snail size.

The rectangular geometric model overestimated pedal area by as much as 35% (Table 1). In contrast to the elliptical model, the greatest deviation between the area calculated with the rectangular model and that determined by weighing occurred when the width of the foot was taken as the maximum width (Table 1). The magnitude of that overestimation was negatively correlated with snail size ($r = -0.590$, $df = 18$, $P = 0.006$). However, when the width at one-half foot length was used to calculate rectangular area, the error of overestimation was positively correlated with shell length ($r = 0.478$, $df = 18$, $P = 0.033$; Table 1). Thus, both the magnitude and the size-specific characteristics of the error in estimating pedal area were functions of the parameters used in the geometric models.

Although both the length and the width (and consequently the area) of the foot of *Ilyanassa obsoleta* increased

Table 2

The area (FA) of the foot of *Ilyanassa obsoleta* as a function of shell length (SL): a comparison of techniques.

Procedure for determining area	Regression equation	r^2	df	P
Weighing	*log FA = 2.23 log SL - 0.83	0.956	18	<0.001
Video	*log FA = 2.27 log SL - 0.86	0.953	18	<0.001
Ellipse (A) (maximum foot width)	*log FA = 2.14 log SL - 0.72	0.963	18	<0.001
Ellipse (B) (foot width at ½ foot length)	log FA = 2.29 log SL - 0.94	0.957	18	<0.001
Rectangle (A) (maximum foot width)	log FA = 2.14 log SL - 0.61	0.963	18	<0.001
Rectangle (B) (foot width at ½ foot length)	*log FA = 2.29 log SL - 0.83	0.957	18	<0.001
ANOCOVA:				
H ₀ : Slopes of regression equations are equal	F = 0.39	df = 5,108	P = 0.428	
H ₀ : Elevations of regressions are equal	F = 28.1	df = 5,108	P < 0.001	
* Indicates regressions that are not significantly different (SNK; P > 0.05)				

with increasing shell length (Table 1), the apparent quantitative association of pedal area with shell length varied with the technique employed in estimating that area (Table 2).

DISCUSSION

Although a quantitative assessment of foot morphometry may be central to an understanding of some aspects of the biology of gastropods, the techniques for determining such parameters as area of the pedal surface may either simply not be identified (GAINEY, 1976) or may be only incompletely described (MILLER, 1974b). For example, in one of the more thorough analyses of the adaptive design of prosobranch pedal morphology, MILLER (1974b) simply states that the length and width of a snail's foot "were measured" and that area of the foot was calculated as the area of a rectangle or of an ellipse "depending upon the shape of the foot." No information is provided as to how the linear dimensions of a snail's foot actually were physically determined nor upon what basis a decision was made about which model of the shape of a gastropod's foot was most appropriate for determining the pedal area of a given snail (MILLER, 1974b). These parameters were then used by Miller to characterize the pedal morphometry of an array of species and to relate these morphometric attributes to functional and adaptive parameters of foot form.

It is clear from the present study that not all techniques for the determination of pedal morphometry yield equally reliable estimates of the quantitative properties of gastropod feet. Aside from difficulty in the mechanics of measuring linear features of a motile, fleshy structure, there may also be significant consequences of the selection of a geometric model for estimating an important parameter

such as area of the foot. If one assumes that the photography-weighing procedure yielded a good measure of foot morphometry, then the alternative geometric models for determining pedal surface area can be compared. One obvious conclusion is that a rectangular model of pedal surface is not a very accurate depiction of the morphology of the foot of *Ilyanassa obsoleta*. For all sizes of snails examined, the rectangular model overestimated pedal area (Table 1). The closest correspondence between the rectangular model and the shape of the foot of *I. obsoleta* occurred among the smaller snails when the rectangular dimensions were based upon width of the foot as measured at one-half foot length. However, even under those conditions the rectangular model overestimated pedal surface area by more than 10% (Table 1).

Overall, an elliptical model provided a reasonably good estimate of pedal surface area for *Ilyanassa obsoleta*, but only when the width of the foot was taken as the maximum width (Table 1). When the width was considered as that at one-half foot length [which was Miller's approach (MILLER, 1974b)], the elliptical model underestimated pedal area. The extent of underestimation was greatest among the smaller snails (Table 1), an observation that is consistent with the better relative fit of the rectangular model to the same animals. Thus, although the ratio of foot length to maximum foot width is constant over a range of shell lengths for *I. obsoleta* (DIMOCK, in press), the shape of this snail's foot does change with the size of the animal. Therefore, one would be in error to assume that a single geometric model adequately describes the morphology of this mud snail's foot irrespective of shell size. It is likely that similar size-specific morphometric relationships exist among other species of gastropods.

An analysis of the various regressions of the area of the foot of *Ilyanassa obsoleta* on shell length confirms the supposition that certain techniques are more satisfactory than others for quantifying pedal morphology (Table 2). Although each procedure for estimating area employed in this study would reveal that the area of this snail's foot is a positive function of shell length, the precise quantitative characteristics of that association depend upon how specific morphological parameters are determined. Such quantitative relationships are influenced not only by the selection of a particular geometric model of foot morphology, but also by the way in which a linear dimension may be defined. The use of a procedure such as the photography-weighting technique has the added advantage of obviating any subjective evaluation of whether or not one geometric model is more appropriate than another (MILLER, 1974b).

The weighing of photographic images of snail feet and the microcomputer assisted video camera scanning of the same images yielded quite comparable measures of the original surface area of the foot of *Ilyanassa obsoleta*. Clearly, the photography-weighting procedure is adaptable to numerous laboratory contexts and requires much less sophisticated equipment than does the video scanning system. This photo-morphometric procedure should be useful in an assortment of investigations of various aspects of the biology of gastropods.

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I appreciate the assistance of Dr. Frank Telewski with the video camera scanning procedure. This study was supported by a grant from the Wake Forest University Research and Publication Fund.

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The 1984 Meeting of the American Society of Zoologists and American Microscopical Society, Animal Behavior Society, Biological Society of Washington, Crustacean Society, International Association of Astacology, Society of Systematic Zoology, and Western Society of Naturalists will be held in Denver, Colorado, from December 27-30, 1984. A call for papers went out in April and the deadline for abstracts is August 14, 1984.

Thirteen symposia and refresher courses are tentatively planned, several of which may be of interest to our readers. For detailed information contact Mary Wiley, American Society of Zoologists, Box 2739 California Lutheran College, Thousand Oaks, CA 91360. Telephone: (805) 492-3585.

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The Western Society of Malacologists Meeting

August 16-19, 1984

The 1984 Annual Meeting of the Western Society of Malacologists will be held at Crown College on the Santa Cruz campus of the University of California, located in the Santa Cruz Mountains overlooking the Pacific Ocean. The main emphasis of this year's meeting will be the Natural History of Marine Mollusks of the Eastern Pacific. In addition to the regular program of contributed papers, several special symposia are planned, including ones on Nudibranch Biology, organized by Dr. Terrence M. Gosliner, the Molluscan Fauna of Northwestern Baja California, organized by Dr. Hans W. Bertsch, and Paleoecology and Fossil Mollusks. All persons interested in malacology, paleontology, and (or) conchology are invited to attend.

For pre-registration and call-for-papers forms, please contact: Dr. George L. Kennedy, Conference Chairman, U.S. Geological Survey, 345 Middlefield Road, Menlo Park, CA 94025. Telephone: (415) 323-8111, ext. 2634.

S. Stillman Berry, 1887–1984

Samuel Stillman Berry, Honorary Life President of the American Malacological Union, passed away on April 9, 1984, at the age of 97.

Berry was born in Unity, Maine, on March 16, 1887. Remaining in his very considerable collection of mollusks is the first shell he picked up at Point Judith, Rhode Island, in 1893. His family lived for short periods in New York City, Phoenix, and Montana, seeking a climate suitable for his frail health. In 1897 they finally settled in Redlands, California, which he called his home ever since, spending part of his summers at the family's Montana ranch.

After high school in Redlands, he did undergraduate work at Stanford University (1905–1909), received his Master's Degree at Harvard University in 1910, and returned to Stanford for his PhD, which he received in 1913. His thesis was on the Cephalopoda.

In 1913 he went to work at Scripps Institution of Oceanography where he helped to build their library and, as a consequence, his own collection of natural history books, perhaps the finest remaining in private hands.

He was supported chiefly by his family's 55,000-acre Winnecook Ranch in Montana, of which he was Chief Executive Officer for over 65 years, a record in corporate America. He was thus able to pursue indepen-

dent work in malacology, authoring, from 1906 onward, over 165 papers and an equivalent number of new species. Some 28 genera and species are named in his honor. In addition to his papers on cephalopods, he is particularly noted for his work on chitons and land snails. In later years, he concentrated on the Panamic marine fauna, publishing much of his work in his own *Leaflets in Malacology*. He was also a horticulturist of note, considered an expert on irises and daffodils.

Berry could hold the rapt attention of visitors to his somewhat cluttered Redlands home with lucid stories about his experiences in the San Francisco Earthquake, other adventures, specimens in his collection, books in his library, and the famous naturalists he met during his career, including G. B. Sowerby, III, Robert E. C. Stearns, Addison E. Verrill, Charles T. Simpson, the Rev. Joseph Rowell, and Edward S. Morse. He had an outstanding memory for the details of events long past.

He had very sharp powers of observation, noting morphological features that others had missed. His extensive collection is meticulously numbered and labeled, many lots having slips with extensive, neatly printed notes and comments.

Eugene Coan

Manuscripts

Manuscripts must be typed on white paper, 8½" by 11", and double-spaced throughout (including references, figure legends, footnotes, and tables). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

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References in the text should be given by the name of the author(s) followed by the date of publication: for one author (SMITH, 1951), for two authors (SMITH & JONES, 1952), and for more than two (SMITH *et al.*, 1953).

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c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117-135. In: R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, Calif.

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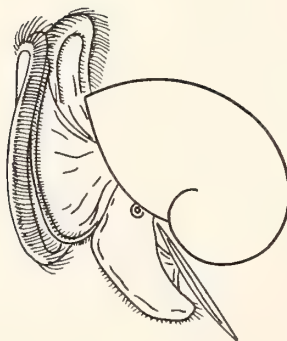
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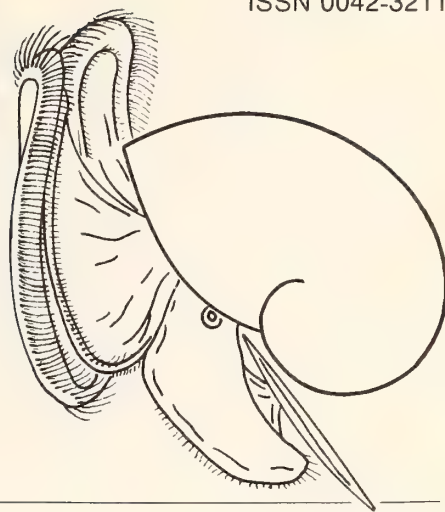
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Very short papers, generally not exceeding 500 words, will be published in a column entitled "NOTES, INFORMATION & NEWS"; in this column will also appear notices of meetings, as well as news items that are deemed of interest to our subscribers in general.

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Culture of the California Red Abalone *Haliotis rufescens* Swainson (1822) in Chile

by

BUZZ OWEN,¹ LOUIS H. DiSALVO,²
EARL E. EBERT,³ AND ERIKA FONCK²

¹ P.O. Box 601, Gualala, California 95445

² Department of Marine Research (DIMAR), University del Norte, Coquimbo, Chile

³ California Department of Fish and Game, Marine Culture Laboratory,
Granite Canyon, Coast Route, Monterey, California 93940

Abstract. *Haliotis rufescens* has been experimentally cultured and maintained during hatchery research in Coquimbo, Chile. Spontaneous spawnings in laboratory populations were observed in spring months from 1979 to 1982, accompanying temperature changes of the ambient seawater. Spawning was artificially induced at various times of the year without conditioning. Broods were produced from both spontaneously occurring and induced spawnings. Once capable of feeding on macroalgae, abalone were reared on the locally abundant *Lessonia flavicans*, although it was experimentally shown that young juveniles grew best when presented with a mixed diet of macro- and microalgae.

INTRODUCTION

THE EXTENSIVE rocky Chilean sublittoral environment, with its cool temperature and rather extensive macroalgae assemblages appears to offer suitable habitat for the growth of abalone, *Haliotis* spp. However, endemic haliotids are unknown in Chile although many other coastlines of the world with similar characteristics host several species of this genus (COX, 1962). The zoogeographical problem of why no haliotids occur in Chile and the possibility of introducing *Haliotis* spp. to Chile as a new marine resource have long interested both Chilean and U.S. researchers. A one-year study, supported by the Organization of American States (OAS), examined the feasibility of bringing an abalone species from California to Chile under quarantined test conditions (EBERT, 1980). In September 1979, about 300 adult and juvenile hatchery-reared *Haliotis rufescens* were brought from California to Chile by two of us (Owen and Ebert), and maintained at the Department of Marine Research (DIMAR), University del Norte, Coquimbo (29°59'S, 71°22'W). Laboratory and field experiments were conducted to examine ecological relationships between the red abalone and endemic Chilean species. Inclusive were studies to determine predator-prey relationships and adequacy of the macroalgae (acceptance, food conversion efficiency, and abalone growth rates). Early in this study some abalone spawned spontaneously; the resulting larvae were reared under impro-

vised conditions. In this report, we document results of this culture and of a later culture from a spawning induced by the methods of KIKUCHI & UKI (1974). We also include data on the comparative growth of small juveniles raised on different diets of Chilean algae.

MATERIALS AND METHODS

DIMAR is located on the northeast margin of Herradura Bay, which is a semi-protected coastal embayment with an oceanic salinity regime. The bay receives negligible freshwater input and sources of contamination are minimal. The temperature range at 10-m depth is typically 13–15°C (ALFSEN, 1979).

Spontaneous Spawning

Several adult abalone, 12 cm in length, which had been in Chile for two weeks, spawned unexpectedly on 22 September 1979 within tanks of continuously renewed seawater at a temperature of 14.4°C. Seawater used as the culture medium for these gametes, larvae, and juveniles was obtained directly from an intake at 10-m depth on the bay bottom. This water was filtered in the laboratory using polypropylene filter bags (GAF Corp.) which retained particles greater than 10 µm. About 3 million eggs from one female were fertilized with about 10 mL of a dense sperm suspension from two males, and the progress of fertilization was monitored by microscopy. After one

hour, fertilized eggs were rinsed to remove excess sperm by three decantations following fresh seawater refills, and were distributed evenly, as judged by sight, to one layer on the plastic pail bottom. Each pail contained 10 L of seawater at 12.5–13.5°C. The static seawater in these cultures rose to air temperature of 17°C over 12 h. Upon reaching the veliger stage, abalone larvae were gently rinsed onto a 52- μ m mesh nylon screen (Nytex; Tetko, Inc., Elmsford, New York), and distributed at several different densities into plastic containers of 10, 20, or 100-L capacity. These culture containers were subject to ambient temperature fluctuations between 13 and 18°C. All seawater was changed daily in the smaller cultures, and one-third the volume was changed daily in the 100-L tanks. Growth and development of larvae were observed daily and mortality was estimated from the quantity of empty shells recovered by screening during seawater changes. Microalgae that settled and grew on container surfaces provided forage. Newly settling larvae were given pure cultures of *Tetraselmis suecica*, and as early growth of post-larvae progressed, pennate diatoms (unidentified) harvested from aquarium surfaces in the laboratory were introduced to the cultures as food.

At a mean size of approximately 5 mm, the abalone juveniles were transferred to 1000-L rectangular fiberglass tanks which received a continuous flow of unfiltered seawater from 10-m depth in the bay. At this time, pieces of *Lessonia flavicans*, *L. nigrescens*, and *Macrocystis integrifolia* were offered to the juvenile abalone, although feeding with microalgae was continued until the young abalone were fully capable of consuming the macroalgae.

Induced Spawning

Abalone were induced to spawn in April 1980 and a controlled rearing experiment was carried out over 12 months. Fertilization and larval rearing were carried out in a heated laboratory at 18–19°C. Seawater was pumped to this laboratory through an offshore sand filter located at 3-m depth on the bay floor. This water was filtered to 10 μ m in the laboratory, and normally had a temperature of 15°C. It was held without further treatment and, after reaching the laboratory temperature of 18°C, was used for the handling of gametes, larvae, and small juveniles.

Two male and two female abalone (6–8 cm in length) that appeared ripe were transferred from holding tanks and placed separately by sex into 20-L plastic pails. These pails were supplied with running seawater at 14°C, fitted with screens on top to prevent crawling out, and left overnight. On the following morning, fecal material was washed from the pails, and the abalone were given a seawater flow of 250 mL/min at 17°C via an ultraviolet (UV) water treatment unit (REFCO Intl., Hayward, CA, model RL-10). The seawater temperature was allowed to rise to 18°C over a 3-h period as treatment proceeded. In a subsequent spawning in September 1980, the same methodology was used, with overnight running seawater

at 13°C and with the temperature of UV irradiated seawater rising from 14 to 18°C over a 3-h period. In both spawnings about 10^6 eggs were retained in 10 L and treated as in the spontaneous spawning. About 25,000 veligers were introduced into each of two 100-L cylindrical fiberglass tanks (3 individuals/cm² of wetted tank surface area) and the rest were discarded. One-third of the water was changed daily in these tanks and a complete rinse was done every 10 days.

Settled abalone were given pure cultures of *Tetraselmis suecica* as required during the first three weeks of culture. After this time, film-forming pennate diatoms were added to the cultures. When juveniles reached an average size of 1.8 mm, they were transferred to seawater trays in a greenhouse. The abalone fed on naturally occurring diatoms that grew in the trays, and upon reaching 5 mm they were transferred to a 1000-L fiberglass tank at a density of about one per 500 cm². There they were maintained on *Lessonia flavicans*.

A spawning was induced in September 1980 to duplicate the April 1980 observations; in this test, only early developmental events were observed. Further spawnings were made during 1980 and 1981 to check on the seasonal condition of abalone brought from California and to note inception of sexual maturity in cultured abalone.

Forage Experiment

Observations of feeding on macroalgae were made to determine which of three Laminariales combined with microalgal films promoted the best growth of juvenile abalone. Five groups of 20 abalone having an average size of 11.2 mm (range = 11.0–11.5 mm) were distributed between five 20-L aquaria receiving a continuous flow of sand-filtered seawater at temperatures of 13–17.5°C.

All abalone were given microalgal films cultured on 15 × 20 cm plastic sheets in the following combinations with species of Laminariales: (Diet A) none, (Diet B) *Lessonia flavicans*, (Diet C) *L. nigrescens*, (Diet D) *Macrocystis integrifolia*, and (Diet E) all three spp. of macroalgae. About 30 g fresh weight of macroalgae pieces were added to each aquarium along with an algae-covered plastic sheet. Microalgal films consisted mainly of pennate benthic diatoms with scattered bluegreen algal filaments and green algal cells. The abalone always had an abundance of food upon which to graze; food was changed routinely to ensure freshness, and fecal matter and debris were siphoned off every other day.

The experiment was run for 75 days, and shell length was measured every 15 days using a millimeter rule, estimating to the nearest 0.25 mm. Abalone were handled using a 10 mm camel's hair brush to avoid damaging their delicate shells. Differences between growth on the different diets were tested for significance using a Model I analysis of variance and a Student-Newman-Keuls (SNK) test (SOKAL & ROHLF, 1969).

Table 1

Parameters of early development of *Haliotis rufescens* obtained in three spawnings in Chile, with comparative values from the literature. h, hours; d, days.

Parameter	Spawnings in Chile			LEIGHTON (1974)	EBERT & HOUK (1984)
	Spontaneous 22 Sept 79	Induced 23 Apr 80	Induced* 9 Sept 80		
Blastula (h)	—	5	5	5	5
Rotating gastrula (h)	16	—	10–12	13	15
Trochophore emergence (h)	22–24	16	16–24	18–24	20
Veliger stage (h)	40	24	29	48	30
Surface tactile stage (d)	5–8	4	3	4	6
Settlement (d)	8–12	4–7	3–7	5–6	7
Notch stage (d)	45	35–40	—	60–70	50
Temperature (°C)	13–18	18	17–19	14–18	15

* Not cultured post-metamorphosis.

RESULTS

Culture Experiments

Spawning: The spontaneous spawning of 22 September 1979 was probably due to one of the small though abrupt rises in water temperature that occur irregularly in waters near Coquimbo during spring and summer months (ALFSEN, 1979). Abalone from the same group spawned spontaneously in their holding tanks on 9 October 1980 when the temperature of incoming water rose overnight from 14.2 to 15.5°C. The phenomenon occurred again on 24 October 1981 when ambient seawater temperature rose from 14.8 to 16°C overnight. In these cases, the female abalone crawled from the holding tanks while simultaneously ejecting ova; males remained below the water surface while releasing sperm.

Abalone were successfully spawned in April, September, and November 1980, and in June, August, and October 1981. In all cases, the abalone spawned within 2 to 4 h after exposure to UV-treated seawater. The spawning of October 1981 included both abalone from California which had been immature when brought to Chile, and abalone cultured in Chile which had reached two years of age. Three-year-old California abalone spawned copiously and produced normal larvae. Of the two-year-old abalone produced in Chile, only 20% exhibited pigmented gonadal tissue. They spawned but produced few eggs, and these failed to be fertilized; no further observations were made on development of sexual maturity in these abalone.

In all spawnings producing viable zygotes, fertilization and early development proceeded in accordance with descriptions in the literature. Some parameters of early development in three cultures are listed in Table 1.

Survivorship and growth: Mortality was negligible in larvae cultures. After the larvae had metamorphosed, a steady attrition of postlarvae began until they neared the 2-mm size. Table 2 lists survivorship and size for the two groups of cultured abalone. In this table it can be seen

that only 0.4% of the abalone in Group II reached the 1.8-mm size from the veliger. However, survival from the 1.8-mm to the 20-mm size neared 50% over the 12 months of observation. Abalone surviving to 35 months reached maximum sizes of 75 mm. All data past 12 months include fortuitous observations outside the original experimental design and represent survival and growth of abalone maintained under less than optimal conditions. Comparisons between the two groups of abalone show an almost equal survival rate when comparing the 6 to 12 month survival of Group I with the 4 to 12 month survival of Group II (Table 2).

Shell color of the cultured abalone was uniformly red and white "candy stripe" to a size of 2 mm. Past this size,

Table 2

Size and age of *Haliotis rufescens* cultured in laboratories at Coquimbo, Chile, and Monterey, California.

Group	Age (months)	Shell length, mm		n
		Mean \pm SD	Range	
I*	6	—	2.0–16.5	—
	12	22.4 \pm 3	14.0–30.0	270
	24	34.5 \pm 5	21.0–48.0	1785
	36	53.8 \pm 6	37.0–75.0	150
II**	2	1.8	1.3–2.2	40
	4	5.9 \pm 1	2.0–10.0	1637
	6	10.9	7.0–16.0	108
	12	20.1 \pm 4	12.0–33.0	970
III***	2	1.8	1.2–2.3	50
	4	5.0	3.0–7.8	50
	6	8.1	4.5–12.4	50
	8	13.0	10.5–16.5	50
	12	20.5	12.2–26.1	50

* Spontaneous spawning; Coquimbo, Chile; Sept. 1979.

** Induced spawning; Coquimbo, Chile; April 1980.

*** Composite of several induced spawnings; Calif. Dept. of Fish and Game, Monterey, California.

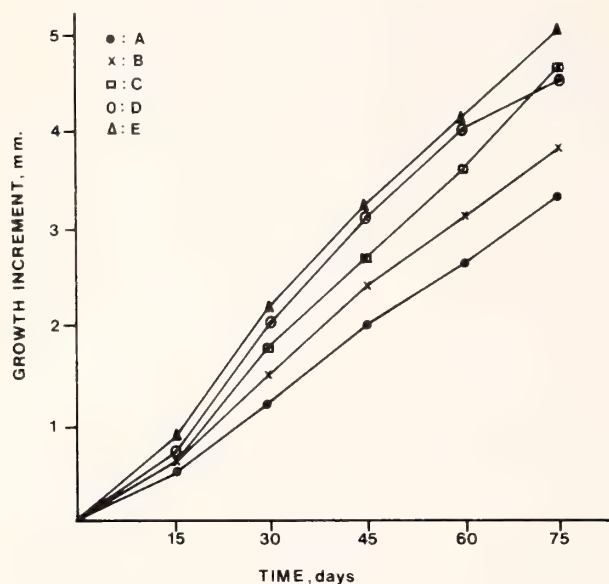


Figure 1

Growth of juvenile abalone on five different algal diets. Each data point represents the mean growth increment for all animals in each treatment. Diets: A = microalgae (ma); B = *Lessonia flavicans* plus (ma); C = *L. nigrescens* plus (ma); D = *Macrocystis integrifolia* plus (ma); E = all macroalgae plus (ma).

a complex variation in color developed among the specimens, including white, green, and red pigment, solidly or in bands. As long as they were provided fresh seawater, forage, and adequate physical space, the abalone appeared hardy and free of disease. Growth was retarded in a group of 5–10 mm abalone that were crowded in a holding tank at a density of 1–2 per 100 cm². In spite of this crowding, the abalone never showed a tendency to crawl out of the tanks. They resumed normal growth when presented adequate physical space.

Feeding experiment: The diet of microalgae alone produced the least growth. Different species of macroalgae gave different growth rates when in combination with

microalgae, and a mixture of all the macroalgae plus microalgae produced optimal growth (Figure 1, Table 3). Statistically significant ($P = 0.01$) differences between groups appeared beginning at 30 days and continued through the end of the experiment (Figure 1, Table 3).

DISCUSSION

Breeder and juvenile red abalone from California acclimated well to ambient seawater conditions at the Coquimbo laboratory. Laboratory tests performed during 1979 and 1980 revealed that the abalone readily accepted native algal species such as *Lessonia flavicans*, *L. nigrescens*, *Durvillea antarctica*, and *Gracilaria* sp. (EBERT, 1979a, b, 1980). Abalone growth, feeding rates, and food-conversion efficiency tests were performed using *L. flavicans*. Juvenile red abalone fed this species grew an average of 10.5 mm in shell length (16.5–27.0 mm) during a 7-month period (EBERT, 1980). This compares favorably with juvenile red abalone growth rates observed in California when giant kelp, *Macrocystis* spp., a preferred food for adults, is fed. The juvenile red abalone feeding rate and food-conversion efficiency on *L. flavicans* during the same 7-month period noted above averaged 7.57% and 9.36% of their body weight/day respectively (EBERT, 1980). Our spawnings showed that at least a portion of the group was ripe throughout the year, suggesting that these animals were fecund the year around in Chilean water, as shown for this species in its California habitat (e.g., BOOLOOTIAN *et al.*, 1962).

Larvae produced in our first culture settled in 8–12 days, and those of the second and third cultures in 3–7 days (Table 1). The longer delay of the first culture was unusual and may indicate stress due to temperature variation under the improvised conditions available at the time. In subsequent cultures where water temperatures were stable, settling time was comparable to literature values. Early abalone development rates in Chile were similar to those observed in California, although a direct comparison is somewhat obscured by the variable culture temperatures within and among the various studies (Table 1).

No mass mortalities were ever experienced at any stage

Table 3

Mean sizes of abalone for which incremental growth data are plotted in Figure 1. At time zero, for all abalone $\bar{x} = 11.2$, $s = 2.5$, $n = 20$. N, total number per treatment; \bar{x} , mean length; s , standard deviation.

Diet ¹	Time, days														
	15			30			45			60			75		
	\bar{x}	s	n	\bar{x}	s	n	\bar{x}	s	n	\bar{x}	s	n	\bar{x}	s	n
A	11.7	0.34	20	12.4	0.40	20	13.2	0.55	20	13.8	0.47	20	14.5	0.64	20
B	11.8	0.29	20	12.7	0.41	20	13.6	0.52	20	14.3	0.52	20	15.0	0.72	20
C	11.8	0.29	20	13.0	0.43	20	13.9	0.55	20	14.8	0.57	20	15.8	0.60	20
D	11.9	0.22	20	13.2	0.41	20	14.3	0.50	20	15.2	0.66	20	15.7	0.68	18
E	12.0	0.29	19	13.4	0.41	19	14.4	0.44	19	15.3	0.66	18	16.2	0.83	18

¹ See Figure 1.

in our cultures in Chile, although the constant low level attrition of postlarvae produced an overall low survival to the 2-mm size. At the time the first respiratory pore appeared, mortality abated. A similar pattern is usually found in California abalone culture research and hatchery operations. California cultivators occasionally experience high postlarval mortalities, presumably from pathogenic bacteria. California hatchery operations also suffer high mortalities in early juvenile stages due to food depletion by copepods and depredation by nematodes and other small invertebrates. For example, the copepod *Tigriopus californicus* competes with young abalone for forage and space and degrades water quality. The role of nematodes is poorly understood, but they are commonly observed feeding on weakened and freshly dead abalones. None of these problems was apparent in Chile. Successful hatchery production of this abalone in Chile will rely in part on solution of the postlarval attrition problem.

Few abalone of any size were lost due to their crawling out of the tanks (often a serious problem in some California hatcheries), even at densities as high as one individual (\bar{x} = 22 mm long) per 70 cm² tank space. At this density, microalgal films were rapidly eliminated, probably depriving the abalone of critical nutrition, thereby stunting their growth. SHIBUI (1972) found diatoms to be the optimum food for *Haliotis discus hannai* in the 3 to 10 mm size range.

Mean growth rates in Chilean produced *Haliotis rufescens* are similar to those observed in California, at least during the first year of life. A wide size range is apparent from all groups of similar age abalone (Table 2).

To our knowledge, this is the first experience of culturing a northern hemisphere haliotid in the southern hemisphere. These preliminary results suggest there are no reasons to preclude success in development of *Haliotis* cultures in Chile. The lower labor costs and present lack of legal restrictions may make this culture economically attractive in Chile in the future. The fate of red abalone introduced to the Chilean sublittoral has not been examined. Experimental plantings in suitable habitats have yet to be conducted. However, laboratory and field experimentation made during the OAS project (EBERT, 1980) gave indications that such transplants would be successful and ecologically compatible with the Chilean nearshore environment. However, further experimentation is recommended, with a male-only population, prior to any

decision to introduce *H. rufescens* to natural Chilean marine environments.

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Multivariate Analysis of Geographic Variation in *Cypraea caputserpentis* (Gastropoda: Cypraeidae)

by

BRIAN N. TISSOT¹

Biological Sciences Department, California Polytechnic State University,
San Luis Obispo, California 93407

Abstract. A multivariate analysis of geographic variation in *Cypraea caputserpentis* Linnaeus, 1758, was initiated to describe morphological variation within and between populations based on adult shell morphology. Variation within samples from three populations suggests that geographically distant populations display similar morphological variability in size, degree of lateral and basal callosity, and number of basal teeth. Although other factors are probably involved, some intralocality variation in size and callosity appears to be related to the degree of exposure to waves and currents. Variation in the number of basal teeth is suggested to be a sexual dimorphism.

Along the east and west coastlines of Australia and southeast Africa, in areas of range-limiting temperature gradients, *Cypraea caputserpentis* displays clines in shell shape. Along these clines, shell form becomes progressively more juvenilized and is correlated with decreasing surface seawater temperatures. Specimens of *C. caputserpentis* from the Hawaiian Islands are distinctly smaller and more marginated, and possess more numerous basal teeth than individuals from the Indo-Pacific. This unique variation does not appear to be related to differences in habitat or surface seawater temperatures. Rather, it is suggested that reproductive isolation of populations in Hawaii has led to the evolution of a morphologically distinct subspecies, *C. caputserpentis caputophidii* Schilder, 1927.

Geographic variation is similar to variation within populations and thus supports the hypothesis that characters variable within populations are adaptively neutral traits likely to be divergent between populations.

INTRODUCTION

COWRIES comprise a large group of gastropods characterized by their colorful, glossy shell and elongate aperture lined by rows of teeth. As with most gastropods, cowries display high diversity in shell morphology. Numerous subspecies display striking examples of infraspecific divergence (SCHILDER, 1967; SCHILDER & SCHILDER, 1938-1939, 1971). Compounding this genetic variation are high levels of geographic, ecological, and sexually dimorphic variation (BROCK, 1980; BURGESS, 1970; FOIN, 1972; LIVERSIDGE, 1968; ORR, 1959; RENAUD, 1976; SCHILDER, 1961, 1962, 1969; SCHILDER & SCHILDER, 1961, 1968). Thus, morphological variation within species can be derived from several sources.

As a result of high variability and a general disagree-

ment regarding the taxonomic importance of shell characteristics, the taxonomy of cowries is large and confusing. Subspecies are described for most of the 200 species, numerous species being associated with five or more infra-specific taxa (ALLAN, 1958; SCHILDER & SCHILDER, 1938-1939, 1971). However, few of these subspecies are recognized by many authorities (BURGESS, 1970; FOIN, 1976; KAY, 1979; TAYLOR & WALLS, 1975). Clearly, in order to establish conservative taxonomic characters, relationships between variation in shell morphology and infraspecific divergence need to be established.

The serpent's head cowry, *Cypraea caputserpentis* Linnaeus, 1758, represents a good example of a morphologically variable species associated with a confusing taxonomy. Pronounced geographic variation is evident throughout the broad Indo-Pacific range of this species (ALLAN, 1958; CATE, 1964, 1969; GRIFFITHS, 1958; SCHILDER & SCHILDER, 1938-1939). In addition, considerable morphological variation is found between individuals within populations (BURGESS, 1970; KAY, 1957, 1960).

¹ Present address: Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92717.

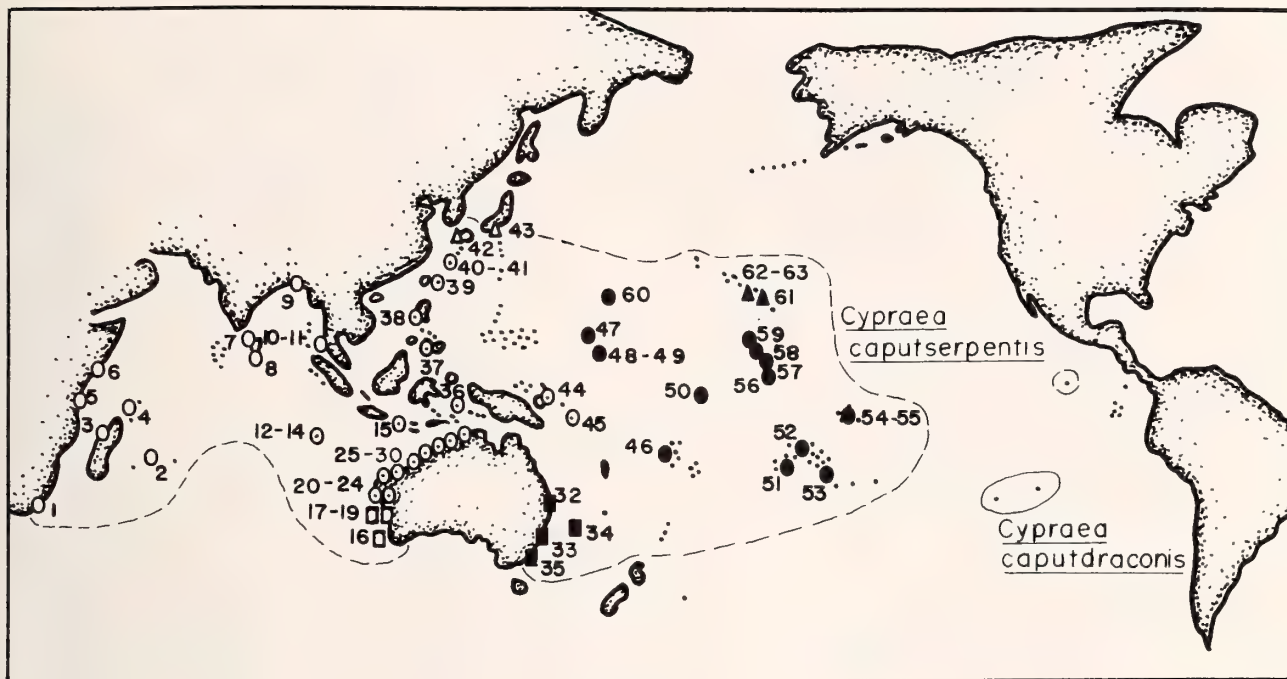


Figure 1

Geographic distribution of *Cypraea caputserpentis* and *C. caputdraconis*, and the distribution of samples used in the statistical analyses. Subspecies described by SCHILDER & SCHILDER (1938-1939:135) are represented by symbols to facilitate reference to Table 1.

As a result, this species is highly variable both within and between populations.

The taxonomy of *Cypraea caputserpentis* reflects this compounded morphological variation—as many as 15 taxa have been associated with this species. SCHILDER & SCHILDER (1971:65) recognize four taxa: one widely distributed subspecies (*C. caputserpentis caputserpentis*) formerly divided into Indian Ocean, west Pacific, central Pacific, and Japanese subspecies (SCHILDER & SCHILDER, 1938-1939); two clines along the east and west coasts of Australia (*C. c. caputanguis* Phillipi, 1849, and *C. c. kenyonae* Schilder & Schilder, 1938, respectively), and one restricted subspecies (the Hawaiian *C. c. caputophidii* Schilder, 1927). In addition, *C. caputdraconis* Melvill, 1888, a species endemic to Easter Island and nearby Sala y Gomez, is believed to have been derived from *C. caputserpentis* (REHDER, 1980; SUMMERS, 1975; TISSOT, 1981) (Figure 1).

The purpose of this study is to describe morphological variation within and between populations of *Cypraea caputserpentis*. Using a combination of univariate and multivariate statistical techniques, this study focuses on describing patterns of variation within and between samples from populations, correlations of patterns with likely causal factors, and an evaluation of infraspecific divergence. Hypotheses relating to causal factors associated with morphological variability are generated based on patterns of

geographic variation, morphological trends in other cowries, and similar morphological patterns in other marine prosobranchs (see GOULD & JOHNSTON, 1972). An additional goal of this study is to test KLUGE & KERFOOT's (1973) premise relating character variability and divergence within and between populations; their theory makes predictions on the origins of geographic variation and suggests relationships between fitness and character variability.

MATERIALS AND METHODS

Specimens of *Cypraea caputserpentis* were obtained from a variety of sources (Table 1). Fully adult specimens with well developed basal teeth and terminal ridges were selected at random from large samples for measurement. The analysis included 717 shells from 63 samples (Figure 1).

Shell characters were selected primarily on the basis of putative subspecific differences (SCHILDER & SCHILDER, 1938-1939) and variables describing shell shape and form. Eighteen variables were measured (Figure 2). Shell color was assessed qualitatively. In addition, for the general area of each collection locality, yearly minimum, maximum, and average surface seawater temperatures were obtained from EBER *et al.* (1968), SVERDRUP *et al.* (1942), the U.S. NAVY (1944), and WYRTKI *et al.* (1971).

Table 1

Description of *Cypraea caputserpentis* sample localities. Locality numbers are mapped in Figure 1.

Locality no.	Locality	Source & ID no.*	Subspecies**	Specimens used in analysis
1a	Natal, South Africa	SAM #4739	CAP	5
1b	Perrier Rocks, Natal, S. Africa	SC	CAP	5
2	Point Aux Sables, West Mauritius	ANSP #273662	CAP	10
3	South side of Nossi Iranji, NW Madagascar	ANSP #257119	CAP	10
4	Seychelles	ANSP #266263	CAP	10
5	Kiwengwa, Zanzibar	ANSP #212418	CAP	10
6	Mogadiscio, Somalia	ANSP #673870	CAP	10
7	Dehiwala Village, West Sri Lanka	ANSP #224983	CAP	10
8	Galle, South Sri Lanka	ANSP #210793	CAP	10
9	Near Calcutta, India	SC	CAP	8
10	Phuket Island, Thailand	ANSP #285855	CAP	10
11	Phuket Island, Thailand	SC	CAP	10
12	Direction Island, Cocos-Keeling	ANSP #288437	RET	10
13	Cocos-Keeling	USNM #589098	RET	10
14	Cocos-Keeling	AMS #c.132845	RET	10
15	Bali	RF	RET	10
16	Radar reef, west Rottne Island	WAM #1473-81	KEN	10
17	East Wallaby Is., Abrolhos Islands	WAM #1470-81	KEN	35†
18	Sunday Is., SE of Dirk Hartog Is.	WAM #1469-81	KEN	10
19	North end Dorre Island	WAM #1468-81	KEN	10
20	Quobba Point	ANSP #238540	RET	10
21	Point Charles	ANSP #267948	RET	10
22	Cape Cuvier	ANSP #267817	RET	10
23	Four miles north of Red Bluff	ANSP #268055	RET	10
24	Bill Bay	WAM #1472-81	RET	10
25	South end Flacourt Bay, Barrow Is.	WAM #394-67	RET	10
26	Kendrew Is., Dampier Archipelago	WAM #1467-81	RET	10
27	Broome	SC	RET	10
28	Broome	WS	RET	10
29	Beagle Bay	AMS #c.85458	RET	10
30	Sunday Island	WAM #1471-81	RET	10
31	Yampi Sound	WAM #1466-81	RET	10
32	Fairfax Island	AMS #c.69053	ANG	10
33	Wooli	AMS #c.101321	ANG	10
34	Long reef, Sydney	AMS #c.75444	ANG	10
35	Lord Howe Island	AMS #c.109335	ANG	10
36	Latuhallalat, Ambon	JWW	RET	10
37	Cebu	TSS	RET	10
38	Chiquita Island, near Subic Bay	BNT #225-232	RET	10
39	Ishigaki Shima	EAK	RET	10
40	Okinawa	USNM #670301	RET	10
41a	Bolo Point, Okinawa	VP	RET	15††
41b	Bolo Point, Okinawa	SC	RET	6††
42	Tanabe, Nagasaki	ANSP #119907	MIK	10
43	Kii, Japan	SC	MIK	10
44	Rabaul, New Britain	SC	RET	10
45	Ranonggar, Solomons	SC	RET	10
46	Fiji	RF	ARG	35†
47	Kwajalein	SC	ARG	10
48	Majuro	SC	ARG	10
49	Majuro, leeward side	EAK	ARG	10
50	Reef West, Canton Island	USNM #617097	ARG	10
51	Paea, Tahiti	SC	ARG	10
52	Taiaro	EAK	ARG	8
53	Raroia	EAK	ARG	10
54	Marquesas	ANSP #80037	ARG	10
55	Taiohae Bay, Nukahiva	USNM #700183	ARG	10
56	Jarvis Island	ANSP #315681	ARG	10

Table 1 (Continued)

Locality no.	Locality	Source & ID no.*	Subspecies**	Specimens used in analysis
57	Christmas Is.	EAK	ARG	10
58	English Harbor, Fanning	EAK	ARG	10
59a	Palmyra Island	USNM #348454	ARG	5
59b	Palmyra Island	USNM #487392	ARG	6
60	Wake Island	EAD	ARG	35†
61a	Honokahua Bay, Maui	JRS	PHI	6
61b	Honokahua Bay, Maui	BNT	PHI	3
62	Fort Kamehameha Reef, Oahu	SC	PHI	10
63	Honolulu Harbor, Oahu	AMNH	PHI	10
				Total 717

* Sources are abbreviated as follows: ANSP, Academy of Natural Sciences, Philadelphia; AMNH, American Museum of Natural History, New York; AMS, The Australian Museum, Sydney; BNT, Brian N. Tissot; EAD, Edward A. Dunlap; EAK, E. Alison Kay; JJW, J. J. Wenno; JRS, John R. Steinbeck; RF, Robert Faniel; SAM, South African Museum, Cape Town; SC, The Shell Cabinet, Falls Church, VA; TSS, The Shell Shop, Morro Bay, CA; USNM, United States National Museum, Washington, DC; WAM, The Western Australian Museum, Perth; WS, Westralian Shells, Broome, WA; VP, Viola Perrault.

** Samples are classified to subspecies according to SCHILDER & SCHILDER (1938-1939:135) to facilitate reference to Table 3. Subspecies are represented by symbols in Figure 1. The following acronyms are used: CAP, *Cypraea caputserpentis caputserpentis* Linnaeus, 1758; KEN, *C. caputserpentis kenyonae* Schilder & Schilder, 1938; ANG, *C. caputserpentis caputanguis* Philippi, 1849; RET, *C. caputserpentis reticulum* Gmelin, 1791; ARG, *C. caputserpentis argentata* Dautzenberg-Bouge, 1933; MIK, *C. caputserpentis mikado* Schilder & Schilder, 1938; PHI, *C. caputserpentis caputophidii* Schilder, 1927.

† Used in single sample analyses. For between sample analysis, sample size was randomly reduced to 10 individuals.

†† Used in juvenile analysis.

The data were examined using a combination of univariate, multivariate, and trend analyses. Due to small sample sizes the canonical analysis of discriminance could not be used as in previous analyses (TISSOT, 1981).

Univariate methods consisted of analysis of variance between groups and a Student-Newman-Keuls multiple range test for each variable. One-way analysis of variance was used to determine significant differences for each variable between localities. Significant variables were analyzed by Student-Newman-Keuls multiple range tests (SOKAL & ROHLF, 1969) to separate localities into homogeneous subsets for each character.

Variation within and between samples was analyzed using principal component analysis (PCA). Variables in this study had different units of measurement (*i.e.*, mm or degrees), and, therefore, the data were transformed to z-scores prior to analysis by PCA. Variation within three samples was examined using multigroup PCA (PIMENTEL, 1979). This technique involves the comparison of angles (PIMENTEL, 1979) or correlations (RUMMEL, 1970) between sample principal components and components derived from pooled within-group dispersion (*i.e.*, pooled correlation matrix). Sample components that display significant correlation with those of pooled dispersion describe similar intralocality variation.

In a second analysis of variation between samples, data were examined by nonmetric multidimensional scaling (MDS). MDS is a nonlinear, nonparametric, iterative multivariate technique that resolves small group differ-

ences and provides a better placement of individuals relative to each other than does PCA (ROHLF, 1972; PIMENTEL, 1981). In this study, results of analysis by MDS are contrasted with results obtained using PCA.

The multivariate technique of canonical correlation was used to determine correlations between shell morphology and seawater temperature as previously observed in cowries (BROCK, 1980; FOIN, 1972; LIVERSIDGE, 1968; SCHILDER, 1961; WILSON & SUMMERS, 1966). Canonical correlation maximizes linear correlations between two related data sets. Dimensions are defined to portray the largest correlations between data sets relative to no correlation within data sets. Examples of this approach can be found in CALHOON & JAMESON (1970), MURPHY (1972), and PHILLIPS *et al.* (1973).

Trends in geographic variation were examined by polynomial trend surface analysis (PTSA), a technique that reduces large data sets to visual patterns, which often provide insight into underlying causal factors contributing to geographic variation (MARCUS & VANDERMEER, 1966). PTSA consists of fitting a least-squares polynomial surface to the data so that coordinates of a locality (latitude and longitude) can be used to predict the value of a variable. This variable can be a single character or a multivariate measure such as a principal component score or MDS axis coordinate (SNEATH & SOKAL, 1973; THORPE, 1976). PTSA models are fitted for various degree polynomials, with residual variation and the proportion of variation explained by each trend surface providing aids

for interpretation (MATHER, 1976). Geographic trends are represented by the contour plot while local variation and sampling error are displayed in the residuals (MARCUS & VANDERMEER, 1966).

The analyses were made using the computer systems at California Polytechnic State University, San Luis Obispo, California. The computer program DISANAL (PIMENTEL, 1979) was used for the analysis of variance, Student-Newman-Keuls multiple range test, and PCA. The program BMDP-6M (DIXON & BROWN, 1979) was used for the canonical correlation analysis. Programs MDS and PTSA, both based on algorithms in MATHER (1976) modified by Pimentel, were also used.

RESULTS

Principal component analysis of three single samples and their pooled dispersion produced principal components significantly correlated ($P \leq 0.05$) with components derived from an analysis of all 63 samples (Tables 2, 4). Thus, geographic variation between samples involves traits also variable within samples derived from three localities.

Variation within Samples: Multigroup PCA

Patterns of variation within samples from three populations—Fiji, Wake, and Wallaby (samples #46, 60, and 17 respectively, see Figure 1)—were analyzed using multigroup PCA. These samples were selected because they were large, each consisting of 35 individuals, and geographically distinct. The goal of this analysis is to examine similarities and differences in morphological variation occurring *within* samples from single populations.

Sample correlation matrices are significantly different (test of homoscedasticity, $P < 0.01$). Results of PCA² on each sample and their pooled dispersion indicate that three components for each sample and four for pooled dispersion describe a large percentage ($>70\%$) of the total variation among variables and individuals (Table 2). In addition, interpretive aids for PCA (PIMENTEL, 1979) indicate that these components have high correlations with the original variables, and possess significantly different eigenvalues. Thus, the following components describe most of the meaningful information derived from variation within the data.

The first component derived from pooled dispersion accounts for almost 50% of the total variation and describes variation attributable to differences in general size of mature cowries (Table 2). A small eigenvector coefficient for shell angle indicates that lateral callosity (shell material added laterally) is independent of size; hence, shell shape is not appreciably different between large and small individuals. Size variation in all three samples is very similar: first components of all samples and pooled dispersion are significantly correlated (all $r > 0.98$).

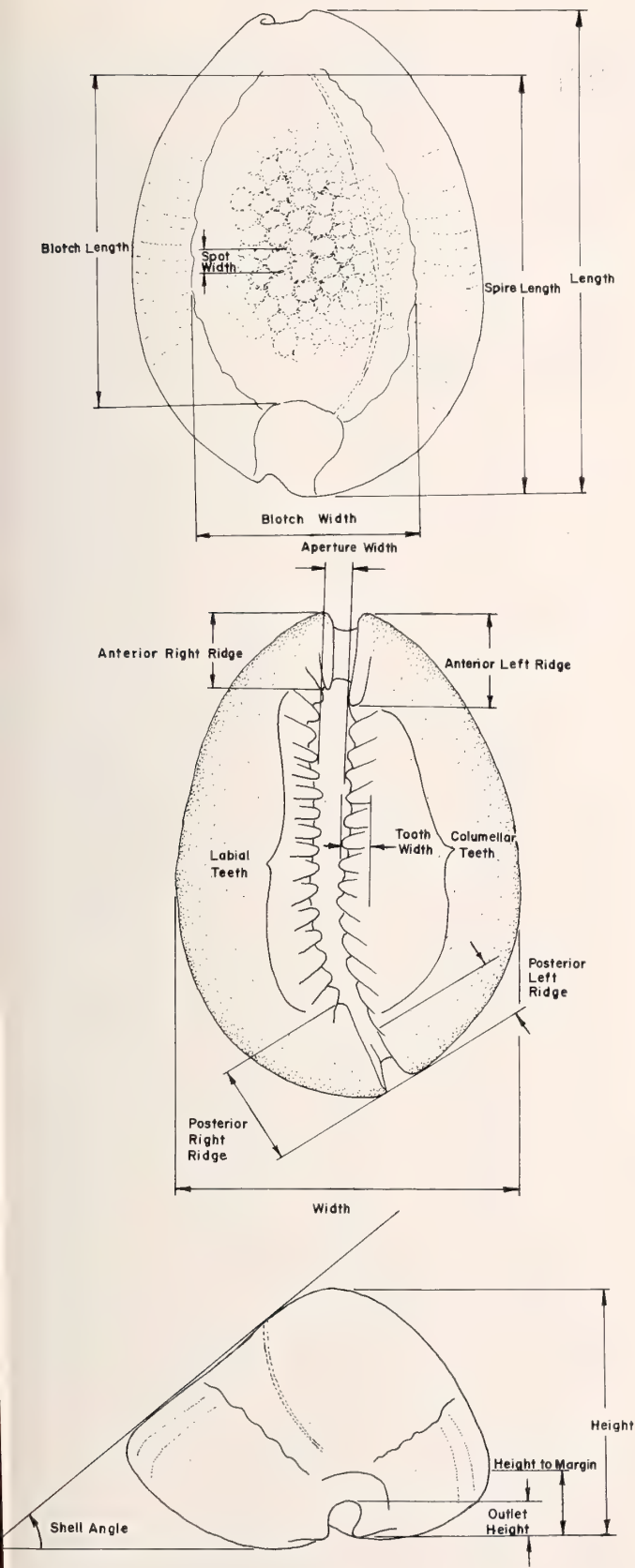
Table 2

Variation within samples of *Cypraea caputserpentis*: principal components derived from pooled dispersion of three samples: Wake, Fiji, and Wallaby. Minor eigenvector coefficients have been omitted for clarity.

Variable	Eigenvectors for principal components			
	1	2	3	4
	General size	Lateral callosity	Basal callosity	Number of basal teeth
Length	0.331	—	—	—
Width	0.311	—	—	—
Height	0.310	—	—	—
Spire length	0.326	—	—	—
Dorsal blotch length	0.311	—	—	—
Dorsal blotch width	0.275	−0.228	—	—
Shell angle	—	−0.570	—	—
Aperture width	0.163	−0.342	—	—
Height to margin	0.139	—	0.541	−0.419
Anterior right ridge	0.238	0.311	—	—
Anterior left ridge	0.282	—	—	—
Posterior right ridge	0.239	0.228	—	—
Posterior left ridge	0.237	—	—	0.464
Number of labial teeth	0.178	—	—	−0.407
Number of columellar teeth	0.150	—	0.407	−0.576
Length of columellar tooth	0.157	—	−0.546	—
Outlet height	0.206	−0.315	—	—
Width of dorsal spot	—	−0.323	—	—
Percentage of total variation	48.8	13.2	6.5	5.7
Cumulative variation	48.8	62.0	68.5	74.2

Variation in shell shape is described by the second and third components of pooled dispersion. Pooled dispersion separates shape variation into two distinct components: differences between individuals in the degree of margination (lateral callosity), and variation attributable to the shape of the base (basal callosity) (Table 2). Variation in lateral callosity is indicated by large eigenvector coefficients for shell angle and blotch width; all three samples have components describing variation in lateral callosity. Differences in basal callosity, described by variation in the height of the base to the margin and length of the mid-columellar teeth (see Figure 2), is evident in components derived from the Fiji and Wallaby samples. Thus, variation in adult shell shape is very similar in each sample.

² Detailed output available from author upon request.



The only difference is the absence of variation in basal callosity between individuals in the sample from Wake Island.

The fourth principal component of pooled dispersion depicts further similarity between samples describing variation in the number of basal teeth and, to a lesser extent, basal callosity (Table 2). PCA of all three samples produced components describing similar variation ($r > 0.68$). In general, individuals with more numerous labial and columellar teeth possess a more callous base.

Variation between Samples: Univariate Analysis

The results of a one-way analysis of variance for each variable showed significant differences among the 63 samples for all 18 variables (all $P < 0.01$). A Student-Newman-Keuls multiple range test separated character means into overlapping subsets. There was little congruence between variables in terms of geographic variation. In fact, using single variables it was impossible to resolve geographic patterns using PTSA. Results for two of the most variable characters, shell length and shell angle, will be used as an example (Table 3).

Based on shell length, the multiple range test produced no unique subsets. Rather, all subsets overlap considerably with adjacent subsets indicating large intra- and inter-locality variation (Table 3). Samples composed of small individuals occur primarily in a broad equatorial belt extending from French Polynesia to Sri Lanka, bordered in the Pacific by the Hawaiian and Ryukyu Islands to the north and Indonesia to the south. The largest shells of this species are found in the Cocos-Keeling Islands, east Africa, New South Wales (Australia), and Western Australia. The largest shell measured 44.2 mm (Bill Bay, Western Australia), the smallest adult 19.5 mm (Moorea, French Polynesia).

Based on shell angle the multiple range test separated samples into three homogeneous subsets (Table 3). Shells with large angles are unmarginated and inflated, all juvenile characteristics, and are found among individuals from the southern range extremes: New South Wales (Australia), South Africa, and Western Australia. Individuals from Woolli and Sydney, both New South Wales, have large shell angles significantly different from each other and from those found in other areas (Table 3). Thus, a steep cline in shell shape is evident along the east coast of Australia.

Variation between Samples: Multivariate Analysis

Results of PCA on 63 samples (621 individuals) are found in Table 4. Interpretive aids indicate that the first

Figure 2

Morphometric variables used to describe the shell of *Cypraea caputserpentis*. Drawing by David W. Behrens.

Table 3

Variation between samples of *Cypraea caputserpentis*: Student-Newman-Keuls Multiple Range Test for two morphological variables: shell length and shell angle. Non-significant ranges are connected by a vertical line. For a description of locality numbers and subspecific designations see Table 1.

Shell length				Shell angle			
Locality no.	Subspecies	Mean value	Significant ranges	Locality no.	Subspecies	Mean value	Significant ranges
49	ARG	26.7		51	ARG	42.3	
37	RET	27.1		14	RET	44.3	
51	ARG	27.6		36	RET	44.4	
44	RET	27.7		10	CAP	44.8	
28	RET	27.8		50	ARG	45.4	
45	RET	27.9		42	MIK	45.5	
61	PHI	28.1		12	RET	45.7	
62	PHI	28.1		49	ARG	45.8	
7	CAP	28.2		9	CAP	46.0	
2	CAP	28.5		45	RET	46.2	
58	ARG	28.7		56	ARG	46.2	
63	PHI	29.1		48	ARG	46.8	
15	RET	29.4		13	RET	46.9	
43	MIK	29.4		43	MIK	47.0	
25	RET	29.5		60	ARG	47.3	
47	ARG	29.6		59	ARG	47.5	
36	RET	29.6		57	ARG	47.7	
27	RET	29.9		44	RET	47.7	
39	RET	29.9		8	CAP	47.9	
52	ARG	30.0		3	CAP	48.2	
50	ARG	30.1		55	ARG	48.2	
38	RET	30.3		11	CAP	48.2	
17	KEN	30.4		27	RET	48.4	
54	ARG	30.4		47	ARG	48.5	
46	ARG	30.7		39	RET	48.6	
57	ARG	30.9		15	RET	48.9	
33	ANG	31.0		25	RET	49.0	
40	RET	31.3		53	ARG	49.0	
35	ANG	31.3		55	ARG	49.2	
3	CAP	31.7		26	RET	49.3	
48	ARG	31.8		46	ARG	49.3	
41	RET	31.8		38	RET	49.5	
42	MIK	31.8		24	RET	49.6	
59	ARG	31.9		28	RET	49.7	
6	CAP	31.9		29	RET	50.1	
8	CAP	31.9		37	RET	50.2	
9	CAP	32.0		62	PHI	50.4	
23	RET	32.1		4	CAP	50.5	
20	RET	32.1		61	PHI	50.9	
53	ARG	32.1		5	CAP	51.6	
16	KEN	32.2		21	RET	51.6	
32	ANG	32.4		6	CAP	52.0	
19	KEN	32.4		40	RET	52.0	
24	RET	32.7		18	KEN	52.8	
11	CAP	32.9		32	ANG	53.2	
60	ARG	33.3		63	PHI	53.2	
10	CAP	33.4		23	RET	53.3	
26	RET	33.4		54	ARG	53.4	
31	RET	33.4		41	RET	53.7	
29	RET	33.5		7	CAP	53.9	
5	CAP	33.5		30	RET	54.0	
12	RET	33.7		31	RET	54.0	
22	RET	33.8		20	RET	54.7	
18	KEN	33.9		22	RET	56.3	
21	RET	34.4		58	ARG	57.3	

Table 3 (Continued)

Shell length				Shell angle			
Locality no.	Subspecies	Mean value	Significant ranges	Locality no.	Subspecies	Mean value	Significant ranges
18	KEN	34.5		16	KEN	57.4	
1	CAP	34.7		2	CAP	57.5	
14	RET	34.9		17	KEN	57.7	
13	RET	35.0		35	ANG	58.7	
4	CAP	35.2		19	KEN	60.0	
34	ANG	35.2		1	CAP	62.5	
56	ARG	35.6		34	ANG	69.5	
55	ARG	36.2		33	ANG	73.0	

three principal components describe a large percentage of the total variation among variables and individuals. For this reason three axes were obtained using the MDS algorithm (see MATHER, 1976). Graphs of locality centroids (=multivariate means) based on principal component scores were very similar to ordinations obtained using MDS. Since MDS provided a greater spread of groups and is theoretically preferred over PCA, the MDS ordination will be discussed in reference to the PCA vectors.

The first principal component (Table 4), accounting for approximately 50% of the total variation, separates localities based on differences in mean size. Geographic patterns based on the first component are similar to those described previously using shell length. Equatorial samples do not differ in size, nor do samples in the southern range extremes, which are intermediate in mean size. Individuals from Hawaiian samples, however, are distinctly smaller (Table 3). The extent of variation in general size between geographically adjacent samples and between replicate samples for the same locality was sufficiently great to prevent the use of PTSA in formulating a trend surface analysis of size.

The second principal component contrasts individuals that differ primarily in the degree of lateral callosity, length, size of terminal ridges, and width of aperture (Table 4). These characteristics describe juvenile shell morphology as indicated by a significant correlation ($r = 0.69$, $P < 0.05$) between this component and one describing shape differences between adults and juveniles in a sample from Okinawa. Ordinations of samples on the second MDS axis differentiate east Australian samples from most other samples. Southwest Indian Ocean (Natal and Mauritius) and Western Australian samples are also unique on this axis, although to a lesser extent. A trend surface analysis of sample scores on the second MDS axis displays geographic patterns (Figure 3).

On the trend surface map (Figure 3) numbers ≥ 6 indicate the degree to which an area follows a particular trend, while numbers ≤ 5 indicate the degree to which an area deviates from the trend (i.e., displays the opposite pattern of variation). Dots symbolize values intermediate

in magnitude between two numbers. MDS coordinates of zero (\$ symbol) indicate areas displaying no variability in the pattern being examined.

The trend map in Figure 3 was created using a fifth order polynomial model and explains approximately 70% of the variation between samples present in the second MDS axis. Samples from the equatorial region do not

Table 4

Variation between samples of *Cypraea caputserpentis*: principal components derived from 63 samples (621 individuals). Minor eigenvector coefficients have been omitted for clarity.

Variable	Eigenvectors for principal components		
	1	2	3
	General size	Lateral callosity	Number of basal teeth
Length	0.336	-0.315	—
Width	0.307	—	—
Height	0.324	—	—
Spire length	0.328	—	—
Dorsal blotch length	0.302	—	—
Dorsal blotch width	0.266	-0.290	—
Shell angle	—	-0.570	—
Aperture width	0.195	-0.280	—
Height to margin	0.146	—	—
Anterior right ridge	0.248	0.301	—
Anterior left ridge	0.291	—	—
Posterior right ridge	0.219	0.334	—
Posterior left ridge	0.245	—	—
Number of labial teeth	0.134	—	-0.524
Number of columellar teeth	0.103	—	-0.631
Length of columellar tooth	—	—	—
Outlet height	0.248	—	—
Width of dorsal spots	—	—	—
Percentage of total variation	47.2	13.2	6.9
Cumulative variation	47.2	60.4	67.3

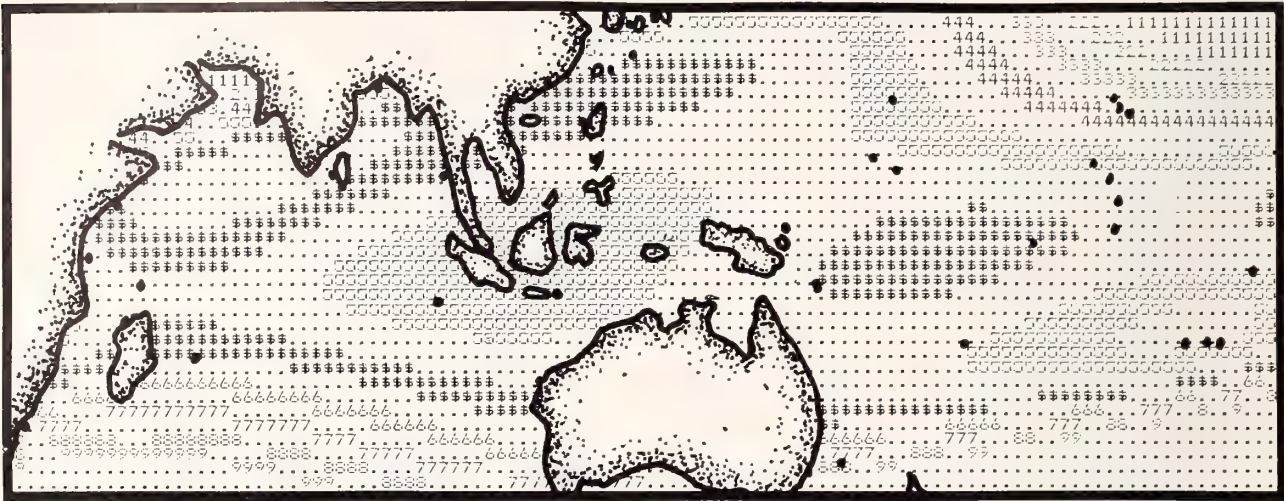


Figure 3

Geographic trends in lateral callosity of *Cypraea caputserpentis* shells: fifth order polynomial trend surface of sample scores on the second MDS axis. Numbers ≥ 6 indicate areas displaying increased juvenilization. Numbers ≤ 5 indicate increasing lateral callosity. The \$ symbol indicates areas displaying neither pattern. Dots symbolize values between two numbers.

exhibit appreciable variation. Rather, the trend applies to all range extremes except Japan. Along the east coast of Australia a steep cline in lateral callosity is indicated by a close spacing of contours and rapid change in numbers. Similar clines exist along the southeast African and west Australian coasts. Southward in these clines, shell shape

becomes progressively more juvenile (see Figure 4). In the Hawaiian Islands the opposite trend is indicated: shells are more margined, smaller, and wider, and have narrower apertures, larger terminal ridges, and more labial teeth.

Using PTSA, additional features of each axis not dis-



Figure 4

East Australian *Cypraea caputserpentis*. Specimens (left to right) are from Fairfax Island, Lord Howe Island, Wooli, and Sydney.

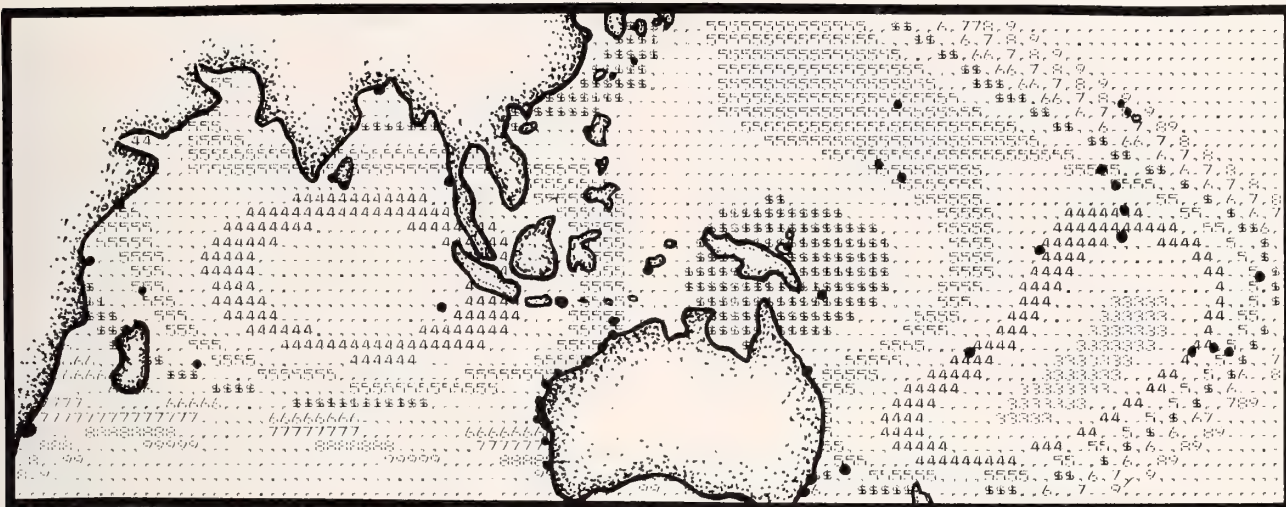


Figure 5

Geographic trends in the number of basal teeth on *Cypraea caputserpentis* shells: fifth order polynomial trend surface of sample scores on the third MDS axis. Numbers ≥ 6 indicate areas displaying an increasing number of basal teeth. Numbers ≤ 5 indicate decreasing numbers of basal teeth. The \$ symbol indicates areas displaying neither pattern. Dots symbolize values between two numbers.

played in the trend map can be obtained by examining the distribution of samples with high residuals. Samples with high residuals on the second MDS axis trend surface are, for the most part, randomly distributed geographically. These samples may represent sampling error, or perhaps locally unique areas.

The third principal component contrasts samples that differ primarily in the number of basal teeth (Table 4). Ordination of samples on the third MDS axis indicates variation is attributable primarily to samples from the Hawaiian Islands. In addition, Wooli (New South Wales, Australia), Natal (South Africa) and two samples from Western Australia also exhibit this pattern of variation.

Trend surface analysis of scores on the third MDS axis (Figure 5) accounts for 63% of the overall variation using a fifth order polynomial model. Clines involving the number of basal teeth are evident between Hawaii and the central Pacific, and to a lesser extent along the southwest Australian and southeast African coasts. Individuals from the Hawaiian Islands differ markedly from the adjacent Line Islands (Figure 5). Samples with high residuals are not geographically randomly distributed on this trend surface. Rather, the residuals serve to contrast specimens from the Line Islands even more strikingly from those of the Hawaiian Islands (*i.e.*, they indicate a steeper cline). Furthermore, the presence of Western Australian and South African clines on the third axis represents artifacts of the methodology; high residuals for the majority of samples on these coasts indicate that clines are an artifact of outliers (*i.e.*, the Rottneest Island and Natal samples). Thus, this axis primarily describes differences due to unique Hawaiian Island samples.

Canonical correlation analysis shows statistically sig-

nificant relationships between shell morphology and seawater temperatures (Table 5). Variable loadings indicate that shell shape (lateral callosity) varies along a temperature gradient. Specimens from the equatorial region, the warmer part of the gradient, possess a wide, margined, relatively low shell. Samples from New South Wales (Australia), Western Australia, and South Africa, the colder regions of the gradient, exhibit unmarginated, inflated shells associated with low surface seawater temperatures. Hawaiian samples do not display this correlation; they ordinate close to the origin. Canonical variate scores are significantly correlated ($r = -0.60$, $P < 0.05$) with second MDS axis scores. Thus, clines in lateral callosity indicated in Figure 3 are significantly correlated with changing surface seawater temperature.

Table 5

Canonical correlation: relationships between shell morphology and surface seawater temperatures as derived from 63 samples of *Cypraea caputserpentis*. Minor variable loadings have been omitted for clarity.

Variable	Variable loadings
Maximum temperature	0.946
Average temperature	0.929
Minimum temperature	0.828
Dorsal blotch length	-0.449
Dorsal blotch width	-0.522
Shell angle	-0.839
Aperture width	-0.485
Canonical correlation	0.788

Variation between Samples: Shell Color

Shell color is also associated with temperature gradients. In general, individuals from the colder regions of the gradient, South Africa, southwest Australia, east Australia, Japan, and Hawaiian Islands, were frequently darker than average and possessed pigmentation in the interstices of the basal teeth. Characteristics such as darkened terminal blotches and the extent of pigmentation near the aperture were also most frequent along the periphery of distribution. Posterior outlet blotch color displayed marked geographic variation: all specimens from the eastern Indian Ocean (*i.e.*, Thailand, India, and Sri Lanka) possessed a rich orange blotch, not the usual pale gray one. A few individuals from Madagascar, Seychelles, and Western Australia also displayed an orange blotch.

DISCUSSION

Results of statistical analyses suggest that variation in size, callosity, and the number of basal teeth is prominent within populations of *Cypraea caputserpentis*. Similar variation is found between populations in the form of mosaics (size), clines (lateral callosity), and disjunct distributions (number of basal teeth). Discussion will first focus on possible causal mechanisms promoting morphological variation within and between populations. Subspeciation and character divergence will then be treated.

Variation within Populations

Multivariate analysis of samples indicates that similar patterns of morphological variation exist within geographically distant populations. These intra-locality variations may represent adaptations to environmental heterogeneity (*e.g.*, VAN VALEN, 1965), random genetic variation independent of significant adaptive value (*e.g.*, DOBZHANSKY *et al.*, 1977), or the result of disruptive selection (*e.g.*, STRUHSACKER, 1968). Results of this study cannot directly distinguish between these, or any other, alternative hypotheses. However, based on studies of other cowries, some inference concerning causal factors promoting morphological variation within populations can be made.

Other than size, the predominant pattern of variation within samples results from differences in shell callosity. Variability in lateral and basal callosity was reported by ORR (1959) for *Cypraea annulus* Linnaeus, 1758, in Zanzibar: wide, heavily callused individuals occur where currents and wave action are strong, and narrow, unmarginated individuals occur in sheltered bays and on muddy reefs. Personal observations on several populations of *C. caputserpentis* in the Philippine and Hawaiian Islands suggest a weak positive correlation between exposure to waves and currents and the extent of overall callosity. As the range of habitats occupied by *C. caputserpentis* is considerably less than that of *C. annulus*, it is not surprising that variation in the callosity of *C. caputserpentis* is less extreme. However, in addition to variation being corre-

lated with exposure, considerable variation in callosity exists between individuals of *C. caputserpentis* collected in the same general area (FANIEL, 1978; personal observations). Although microhabitat differences between individuals may be pronounced, it is not readily apparent that the majority of variation in callosity in *C. caputserpentis* is directly related to environmental exposure gradients as is suggested for *C. annulus* and numerous other species of marine prosobranchs (CROTHERS, 1982; HELLER, 1976; PHILLIPS *et al.*, 1973; STAIGER, 1957; STRUHSACKER, 1968; TISSOT & STEINBECK, 1983; VERMEIJ, 1978).

The number of basal teeth also varies within populations but relationships to environmental or ecological parameters are unclear. Variation in the number of basal teeth could represent an adaptation to predators, although experiments suggest that some major predators (crabs) attack the shell by crushing the dorsal surface (VERMEIJ, 1978). SCHILDER & SCHILDER (1961) find the number of columellar teeth to vary between sexes of *Cypraea moneta* Linnaeus, 1758, and *C. annulus*. Similar morphological variation is also found in *C. spadicea* Swainson, 1823 (Dunn & Tissot, unpublished data). Thus, intralocality variation involving the number of basal teeth in *C. caputserpentis* may represent a sexual dimorphism.

Geographic Variation

Overall size in *Cypraea caputserpentis* follows a geographic trend that has been described for shell length in *C. arabica* Linnaeus, 1758, *C. tigris* Linnaeus, 1758, and *C. errones* Linnaeus, 1758 (FOIN, 1972; SCHILDER, 1961, 1962; SCHILDER & SCHILDER, 1968): a central equatorial zone of small-shelled populations surrounded by populations possessing larger shells at the range periphery. *Cypraea caputserpentis* deviates from this general cypraeid pattern in one major way: populations in Hawaii possess a small shell.

ORR (1959) reported shell length in *Cypraea annulus* to vary inversely with degree of exposure to waves and currents of a sufficient magnitude to 'mask' geographic variation. Personal observations suggest that size variation within populations of *C. caputserpentis* is similar. As a result size displays a mosaic geographic pattern, evidenced by variation between replicate and adjacent samples and the inability of PTSA to fit a global trend map of general size. The implication is that individual size is a result of local parameters (*e.g.*, diet, habitat, wave shock, and water movement) as well as global parameters (*e.g.*, water temperature and distribution of predators).

Clinal variation in the extent of lateral callosity is correlated with changing surface seawater temperatures and parallels the development of adult shell characteristics. Along east Australia, Western Australia, and southeast Africa, individuals within populations exhibit a similar progressive change in shell form as they range south (Figure 4). Other species of cowries (*Cypraea erosa* Linnaeus, 1758, *C. vitellus* Linnaeus, 1758, *C. felina* Gmelin, 1791,

and *C. gracilis* Gaskoin, 1849, in east Australia; *C. marginalis* Dillwyn, 1827, *C. helvola* Linnaeus, 1758, and *C. erosa* on the southeast coast of Africa) appear to exhibit a similar morphological trend (LIVERSIDGE, 1968; SCHILDER, 1969; SCHILDER & SCHILDER, 1938–1939, 1967). Given that all three clines in *C. caputserpentis* display a similar trend, as well as at least six other species of cowries, a common factor is likely to be responsible. As each species occupies different habitats, and presumably has different predators, unique diets, and different dispersal characteristics, it is unlikely that these clines are maintained directly by natural selection. Instead, the induction of juvenile characteristics by environmental parameters is suggested.

Many clines in mollusks appear to result from the effects of water temperature gradients on shell growth and development (FRANK, 1975; LIVERSIDGE, 1968; PHILLIPS *et al.*, 1971; VERMEIJ, 1978; WILSON & SUMMERS, 1966). Cold-water populations of several gastropods show slower growth rates and a longer life span than do warmer water populations (FRANK, 1975; KENNY, 1983). If growth is similar in *Cypraea caputserpentis*, then the proportion of juvenile shells in cold-water populations would tend to increase. Thus, correlations between temperature and growth rate could be a factor promoting clinal variation.

Alternatively, slower growth may induce juvenile characteristics by causing doming of the shell, a result of coiling (VERMEIJ, 1978). This effect, together with the increased metabolic energy required to precipitate calcium in colder waters (SVERDRUP *et al.*, 1942) could explain inflated, unmarginated shell morphology. A growth experiment using individuals from populations along a cline, in which growth rates and reproduction are monitored at several temperatures, could clarify the mechanisms involved. At any rate, correlations between shell morphology and surface seawater temperature suggest that clines in *Cypraea caputserpentis* are for the most part a result of the effects of water temperature on shell growth and development. For this reason the Australian subspecies, *Cypraea c. caputanguis* and *C. c. kenyonae*, should not be recognized as valid taxa.

Geographic variation in the number of basal teeth is largely based on samples from the Hawaiian Islands. Overall, specimens of *Cypraea caputserpentis* from the Hawaiian Islands are different in numerous ways from those in the Indo-Pacific. In contrast to most species of Hawaiian cowries—e.g., *C. tigris* (BROCK, 1980; FOIN, 1972; KAY, 1961a; SCHILDER, 1962)—Hawaiian *C. caputserpentis* are distinctly smaller (Table 3). In addition, Hawaiian shells are more marginated, wider, and darker in color, and have a narrower aperture and larger terminal ridges, a unique situation compared to shells from southern clines associated with similar seawater temperatures (Figure 3). Finally, and perhaps more importantly, basal teeth are remarkably more numerous on Hawaiian shells when compared to those found in other areas, especially from the adjacent Line Islands (Figure 5).

Morphological variation attributable to Hawaiian *Cypraea caputserpentis* does not appear to be habitat related as this species occupies similar habitats throughout its range (unpublished data). In addition, based on canonical correlation analysis, variation does not appear to be temperature related. Given the geographically isolated position of the Hawaiian Islands and the limited dispersal ability of the pelagic larvae (12 h in Hawaiian individuals; KAY, 1957), the morphology of Hawaiian *C. caputserpentis* is a likely result of reproductive isolation from adjacent populations. For these reasons, *C. caputserpentis caputo-phidii* should be recognized as a valid subspecies. Taxonomically these results agree with the univariate study of GRIFFITHS (1958).

Subspeciation

Currents near the Hawaiian Islands flow to the southwest, creating a barrier between Hawaii and the adjacent Line Islands (ZINSMEISTER & EMERSON, 1979). The absence of *Cypraea caputserpentis* from Johnston Island (R. E. Brock, E. A. Dunlap, personal communications), an atoll midway between the Line and Hawaiian Islands, and the predominantly Hawaiian marine fauna at Johnston (BAILEY-BROCK, 1976; BROCK, 1980; BUGGELN & TSUDA, 1966; EDMONDSON *et al.*, 1925; GOSLINE, 1955) suggest colonization from another area. Affinities of the Hawaiian molluscan fauna with those of the west Pacific, as well as the distribution of cowries in the Hawaiian islands, suggest colonization from the west (KAY, 1961b, 1967)—a distance well over 4000 km. One hypothesis, advocated by ZINSMEISTER & EMERSON (1979), suggests a reduction of this large open-water barrier during the Pleistocene when lower water levels created habitable islands from several of the Emperor Seamounts (the northwest end of the Hawaiian chain). Colonization of these islands could have promoted the establishment of populations of *C. caputserpentis* in Hawaii; subsequent submergence would have severed gene flow from the west Pacific. High levels of subspecific endemism in Hawaiian *Cypraea* (38%; SCHILDER & SCHILDER, 1971) also suggest recent isolation and perhaps colonization in a similar manner.

Character Divergence

Significant correlations between principal components derived from single samples with those derived from 63 samples suggest that patterns of morphological variation within populations of *Cypraea caputserpentis* are similar to patterns of geographic variation. This similarity suggests that geographic variation has arisen from population variation, an evolutionary phenomenon advocated by KLUGE & KERFOOT (1973). These authors maintain that character variability within populations is inversely proportional to its effect on fitness; hence, variable characters are more likely to differ between populations as they are adaptively neutral. Divergence between populations in

variable characters occurs in response to directional selection (KLUGE & KERFOOT, 1973) or to environmental effects (SOKAL, 1976, 1978).

Recently ROHLF *et al.* (1983) reported the "Kluge-Kerfoot phenomenon" to be a statistical artifact, a result of calculating coefficients of variation for characters with different units, distributions, and sampling error. The present study, using multigroup PCA, supports Kluge and Kerfoot's premise without using coefficients of variation.

In reference to the biology of *Cypraea caputserpentis*, the existence of the Kluge-Kerfoot phenomenon suggests that intrapopulation variations in size, callosity, and number of basal teeth are adaptively neutral characteristics that have been subject to directional selection and/or different environments between populations, producing geographic variation. This hypothesis can be tested by measuring natural selection within several populations (HALDANE, 1954; LANDE & ARNOLD, 1983) and by undertaking a reciprocal transplant study. The elucidation of mechanisms relating intra- and inter-population variation in *C. caputserpentis*, coupled with an analysis of geographic variation in larval dispersal characteristics, could provide valuable information concerning the development of geographic variation, and the subsequent evolution of species.

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Seasonal Variation in Biochemical Composition of the Fresh-water Pond Snail *Viviparus bengalensis* Linnaeus

by

P. K. GUPTA

Department of Zoology, K.L.D.A.V. College,
Roorkee 247667, India

AND

V. S. DURVE

Department of Limnology and Fisheries, University of Udaipur,
Udaipur 313001, India

Abstract. The seasonal biochemical analysis of the soft body tissues of the fresh-water pond snail *Viviparus bengalensis* Linnaeus was conducted for both sexes to determine water, ash, glycogen, protein, lipids, cholesterol, and total energy values. Water constituted the bulk of the tissue, fluctuating between 79.14 and 83.83%; this variation was related to breeding and environmental factors. Ash content did not exhibit any relation to the reproductive cycle and varied between 125.43 and 212.93 mg/g. Glycogen levels depended on feeding and the reproductive cycle of the snail, as glycogen is utilized in gamete formation; these values varied between 197.57 and 389.37 mg/g. Protein formed the bulk of organic constituents, and values between 341.54 and 581.48 mg/g were recorded. Lipids fluctuated between 34.45 and 121.92 mg/g, and exhibited significantly different levels between the two sexes. Cholesterol levels exhibited a confusing situation; they did not show a definite trend and fluctuated from 120.00 to 221.48 mg/g. The total energy values differed significantly both between the sexes and between seasons; values from 4.514 to 8.568 kcal/g were recorded.

INTRODUCTION

SEASONAL VARIATIONS in biochemical composition are invariably cyclical in nature and closely follow the physiological activities of the animal. Because many mollusks have food value, biochemical studies on them have assumed great importance. These studies on mollusks, apart from providing valuable information on their constitution, also give insights into their body physiology during different seasons of the year.

Biochemical analyses of a number of mollusks have been made by many workers. Several have investigated the biochemical composition of gastropods and related them to the animals' reproductive cycles and environmental factors: MEENAKSHI (1956) for *Pila*, EMERSON (1965) for prosobranch snails, WEBBER (1970) for *Haliotis*, RAO *et*

al. (1972) and CHATTERJEE & GHOSE (1973) for *Viviparus* and *Acrosloma*, STICKLE (1975), and LAMBERT & DEHNEL (1974) for *Thais*.

The seasonal biochemical composition of *Viviparus bengalensis* has not been studied in detail. The present work deals with the monthly biochemical variations in water, ash, glycogen, protein, lipid, cholesterol, and total energy values in relation to this snail's reproductive cycle.

MATERIALS AND METHODS

Specimens of the snail *Viviparus bengalensis* were collected from a pond once a month (preferably in the second week) from January 1979 to March 1980. They were placed in a well-aerated glass aquarium in the laboratory and sorted by sex. Thirty to forty healthy snails of each sex were

sacrificed each month for the study. All of the weighings were done on a microanalytical balance to the nearest 0.001 mg. Except for water content, all the tests were performed on dry tissue, and the results are presented on a dry tissue weight basis. Each sample was analyzed in triplicate or quadruplicate.

To determine the percentage of water, after breaking open the shell the soft body tissue was dried in an oven at 60°C to a constant weight. The difference between pre- and post-dried tissue weight was taken as its water content. Ash contents were determined by ashing the dried, powdered tissue in a muffle furnace at 600°C for 6 h. Glycogen was estimated by the method of SEIFTER *et al.* (1950), using anthrone as the coloring agent and 1.11 as the multiplying factor. Total proteins were determined by the folin phenol reagent method (LOWRY *et al.*, 1951) with bovine albumin Fraction IV as the standard. Soxhlet extractors of 100-mL capacity were utilized for extracting the lipid from the tissue; petroleum ether was the solvent. The method of PEARSON *et al.* (1954) was adopted for the estimation of cholesterol using paratoluene sulfonic acid as the coloring agent. Total energy was determined by burning a known amount of dried and powdered tissue in a bomb calorimeter following LEITH's (1968) method.

The water content is presented as percentage wet weight, the energy values as kcal/g dry weight, and the remaining biochemicals as mg/g dry weight. All of the spectrophotometric readings were carried out on a Systronic MK 105 spectrophotometer. The data were subject to Student's *t*-test for the determination of significance. Standard deviation was calculated by the formula of SNEDECOR & COCHRAN (1967). Significance of the means was calculated by *t*-tests (STEEL & TORRIE, 1960) using a formula appropriate for unpaired observations and unequal variances. Significance levels were set at 0.05 and 0.001%.

RESULTS

Water constituted the bulk of the total wet weight of the body tissue and varied between 79.14 and 83.83%. In males the highest and lowest levels were recorded in December (83.83%) and May 1979 (80.69%) respectively, whereas in females these were in January 1979 (82.28%) and December (79.14%). Water content differed significantly between sexes of the snail ($P < 0.05$) in the months of February, April, May, June, July, and August of 1979, and in March 1980; highly significant differences were recorded in September, October, November, and December of 1979, and in February 1980 ($P < 0.001$). In January and March of 1979, and in January 1980, the difference was nonsignificant (Table 1).

Ash represents the total inorganic contents of the tissue. In males, after recording a peak value of 212.93 mg/g in February 1979, ash declined sharply to its lowest level of 125.43 mg/g in July. In females, ash exhibited its peak level of 194.28 mg/g in January 1979. This peak was followed by a decrease that touched the lowest level of

131.36 mg/g (with the exception of April when suddenly it rose). However, January 1980 yielded a maximum value of 200.51 mg/g. February, March, June, July, September, October, and November of 1979, and February and March of 1980, yielded significant levels of variation, and the difference was highly significant in January 1980 (Table 1).

Glycogen levels were correlated with the reproductive cycle of the snail. During the prespawning and spawning months (January to April) a decrease in glycogen levels was recorded in males. In August, which also happens to be a prespawning month, glycogen reached the highest value of 369.01 mg/g. In the peak spawning month of October, it fell to the lowest level of 197.57 mg/g. In contrast to males, females showed increases in glycogen content from January to March 1979 (the later posting the highest value of 368.11 mg/g). During spawning and postspawning months from April to June, glycogen levels declined rapidly, reaching the lowest value of 251.49 mg/g in June. December and January registered declines as the animal underwent hibernation. The prespawning month of March 1980 recorded a steep rise to 389.37 mg/g. Significant differences between the sexes were observed from January to April, August, September, and November of 1979, and February of 1980; October and December yielded highly significant differences (Table 1; Figure 1).

Protein formed the bulk of the organic content of the tissue in both sexes. The males registered the maximum level of 581.48 mg/g in October and the lowest level of 416.32 mg/g in January 1979. Females recorded their highest protein values in June (576.93 mg/g) and lowest in February (1979). April, September, and October of 1979, and February of 1980, exhibited highly significant differences in protein content between the sexes; for January, June, and July of 1979, these differences were nonsignificant, and for the rest of the period of study they were significant (Table 1).

Like glycogen, lipids also showed seasonal variation in relation to the breeding cycle of the snail. Males recorded the lowest values of 44.56 and 44.86 mg/g in February and March respectively, and the highest value of 77.87 mg/g in November, which is the month of hibernation. Females exhibited an interesting pattern. After recording their highest value of 121.91 mg/g in February 1979, glycogen levels in females declined rapidly and touched the lowest level of 34.45 mg/g in June. There were highly significant differences between the sexes in a majority of the months of study, except for May, July, August, and December of 1979, and March of 1980, when differences were significant (Table 2; Figure 2).

Cholesterol forms an important constituent of lipids and plays a significant role in metabolic processes. The males recorded their lowest values of 134.81 mg/g in March 1979 and their highest in September (221.48 mg/g). In females, after recording the lowest value of 118.51 mg/g in January 1979, a gradual rise in cholesterol content was

Table 1

Monthly variations in water percentage, ash, glycogen, and protein content, reported as mean \pm standard deviation and *t*-values, in the soft tissues of male and female *Viviparus bengalensis* L.

Month and year	Water percentage (wet wt.)			Ash (mg/g dry weight)			Glycogen (mg/g dry weight)			Protein (mg/g dry weight)		
	Male	Female	<i>t</i> -value	Male	Female	<i>t</i> -value	Male	Female	<i>t</i> -value	Male	Female	<i>t</i> -value
Jan. '79	81.71 ± 0.79	82.28 ± 0.74	0.60 NS	192.98 ± 3.87	194.28 ± 1.90	0.10 NS	344.32 ± 6.29	319.73 ± 2.60	0.80*	416.32 ± 7.14	413.56 ± 3.80	0.06 NS
Feb. '79	81.98 ± 0.67	80.63 ± 0.57	2.21*	212.93 ± 4.16	171.65 ± 4.90	1.48*	312.78 ± 3.52	365.22 ± 4.86	2.04*	424.74 ± 5.60	341.54 ± 4.03	2.51*
Mar. '79	81.59 ± 1.31	80.87 ± 0.50	0.48 NS	200.53 ± 3.68	163.35 ± 4.88	1.49*	289.19 ± 1.64	368.11 ± 7.08	2.00*	463.18 ± 6.28	361.60 ± 8.06	1.46*
Apr. '79	81.61 ± 0.93	80.61 ± 0.52	0.99*	185.74 ± 2.95	202.06 ± 5.45	0.61 NS	239.73 ± 4.14	315.13 ± 5.79	2.14*	502.11 ± 1.36	433.61 ± 3.33	7.95**
May '79	80.69 ± 0.72	79.79 ± 0.72	1.05*	134.22 ± 2.44	131.36 ± 3.69	0.19 NS	269.19 ± 5.04	288.24 ± 4.99	0.51 NS	516.52 ± 3.53	526.74 ± 1.81	0.98*
Jun. '79	82.54 ± 0.51	79.80 ± 0.47	6.55**	127.70 ± 2.25	140.69 ± 2.79	1.45*	241.62 ± 4.09	251.49 ± 4.66	0.36 NS	563.47 ± 6.96	576.93 ± 2.15	0.38 NS
Jul. '79	82.76 ± 0.52	82.26 ± 0.46	1.21*	125.43 ± 2.01	154.15 ± 3.37	2.49*	271.35 ± 6.15	266.13 ± 1.66	0.17 NS	538.75 ± 9.88	566.80 ± 4.72	0.34 NS
Aug. '79	83.71 ± 0.50	81.99 ± 0.50	3.82**	130.48 ± 0.89	134.55 ± 3.52	0.39 NS	369.01 ± 7.11	311.46 ± 5.39	1.04*	446.30 ± 4.88	502.26 ± 4.34	1.81*
Sep. '79	82.78 ± 0.38	81.54 ± 0.14	8.97**	136.48 ± 1.60	154.56 ± 2.48	2.73**	281.08 ± 2.08	268.47 ± 3.32	1.05*	421.22 ± 4.47	521.30 ± 3.45	4.45**
Oct. '79	81.99 ± 0.82	79.89 ± 0.38	3.22**	127.77 ± 1.43	149.49 ± 1.87	5.46**	197.57 ± 3.60	305.13 ± 4.68	4.12**	581.48 ± 4.67	459.27 ± 3.32	5.35**
Nov. '79	82.44 ± 0.36	79.72 ± 0.70	4.86**	141.88 ± 2.37	159.69 ± 3.67	1.32*	282.97 ± 6.46	358.38 ± 1.27	2.32*	514.96 ± 3.82	460.82 ± 3.62	2.77*
Dec. '79	83.83 ± 0.73	79.14 ± 0.37	7.88**	162.70 ± 3.07	169.46 ± 2.25	0.65 NS	254.59 ± 4.03	333.51 ± 3.37	3.82**	531.36 ± 4.96	427.11 ± 7.59	1.75*
Jan. '80	81.24 ± 0.85	81.28 ± 0.38	0.06 NS	180.87 ± 1.88	200.51 ± 2.00	3.54**	283.92 ± 4.99	300.54 ± 7.11	0.33 NS	445.19 ± 2.69	422.74 ± 4.47	1.13*
Feb. '80	81.38 ± 0.53	79.93 ± 0.46	3.44**	175.08 ± 2.72	183.37 ± 2.42	0.83*	381.62 ± 4.19	327.30 ± 4.85	1.76*	430.92 ± 3.15	401.76 ± 1.76	3.26**
Mar. '80	81.86 ± 0.52	81.27 ± 0.79	0.79*	159.41 ± 1.18	141.01 ± 6.03	0.73*	375.41 ± 4.27	389.37 ± 7.66	0.24 NS	414.46 ± 3.84	383.16 ± 3.01	1.97*

NS Non-significant.

* Significant ($P < 0.05$).

** Highly significant ($P < 0.001$).

observed, and a maximum value of 197.98 mg/g was reached in June. Highly significant levels of cholesterol were observed in the months of September, October, and November of 1979, and February of 1980; they were not significant in March, April, and August of 1979 and January of 1980, and significant for the remaining months of study (Table 2).

Males exhibited their lowest and highest total energy values in December (5.470 kcal/g) and March of 1979 (8.563 kcal/g) respectively. Females recorded the lowest energy value in March of 1979 (4.514 kcal/g) and the highest value in August (7.441 kcal/g). Highly significant differences were observed for these values for all of the months with the sole exception of February 1980, when the difference was significant, and January 1980, when it was not significant (Table 2).

DISCUSSION

Reproductive cycle and seasonal environmental changes are two main factors influencing the biochemical synthesis and utilization of metabolites. Similarly, changes in abiotic and biotic factors, such as temperature, pH, salinity, humidity, aridity, and availability and type of food in the aquatic ecosystem, are largely responsible for the biochemical variations in the body tissues of the animals living therein.

In the case of *Viviparus bengalensis*, the biochemical variations have been found to be interlinked with its prolonged breeding activity and environmental fluctuations. These snails were collected from a pond with a maximum depth of 2.4 m. The water temperature recorded was 19°C in December, 27°C in April, 32°C in June, and 30°C in September. The pH of the pond water ranged from 7.8

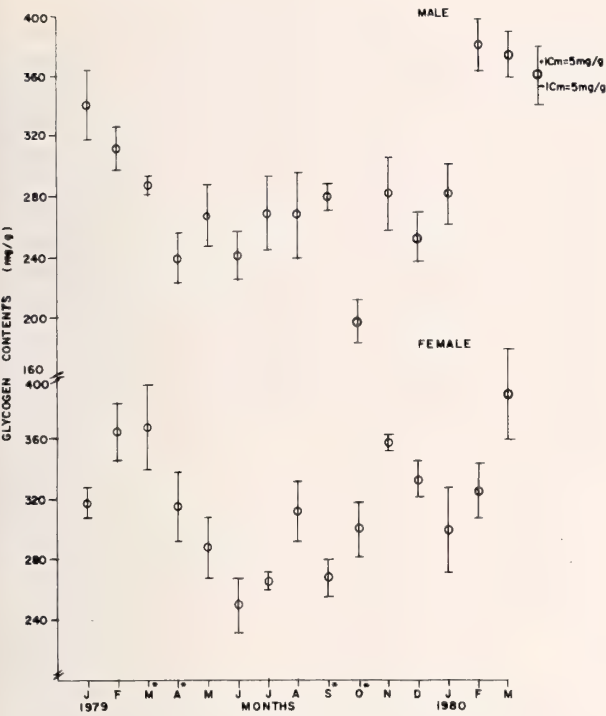


Figure 1

Monthly variations, with standard deviations, in glycogen content of soft body tissue of *Viviparus bengalensis*. *Denotes months of intensive breeding activity.

to 8.1, and the dissolved oxygen was above 5.8 mg/L in every season of the year. The water hardness was 208 ± 6 mg/L. The pond never dried in summer, though the water level decreased, and it never overflowed in the rainy season. In winter when the snails underwent hibernation, water was sufficient to cover the animals.

As is apparent from the results, water formed the bulk of the wet weight of soft body tissue of the snail. Water content decreased in summer and winter months, but rose in the monsoon season. Similar observations were made by CAMPION (1961) for *Helix aspersa*, NAGABHUSHANAM & KULKARNI (1971) for *Laevicaulis alta*, MULEY (1975) for *Melania scabra*, and NAGABHUSHANAM & MANE (1975) for *Kataysia opima*. However, a reciprocal relationship of water with protein, fats, and glycogen, reported by FRAGA (1956) for *Mytilus edulis*, VENKATARAMAN & CHARI (1951) for *Ostrea madrasensis* and *Acrosloma variata*, FUGI (1957) for *Corbicula japonicum*, and DURVE & BAL (1961) for *Crassostrea gryphoides*, could not be established in the present study. However, there were variations in the water percentage in both the sexes (decreasing in summer and increasing in monsoon) at constant temperature and high relative humidity as observed by MULEY (1975).

A relationship between ash content and the breeding cycle could not be established in this snail. It was observed that ash contents were lower in summer and higher in

Table 2

Monthly variations in lipid, cholesterol, and total energy content, reported as means \pm standard deviation and *t*-values, in the soft tissues of male and female *Viviparus bengalensis* L.

Month and year	Lipid (mg/g dry weight)		Cholesterol (mg/g dry weight)		Total energy (kcal/g dry weight)	
	Male	Female	Male	Female	Male	Female
Jan. '79	47.29 \pm 1.70	81.23 \pm 1.75	149.63 \pm 3.22	118.51 \pm 3.67	5.584 \pm 0.085	6.651 \pm 0.144
Feb. '79	44.56 \pm 1.53	121.91 \pm 3.07	160.00 \pm 3.17	134.01 \pm 1.60	6.296 \pm 0.223	5.588 \pm 0.111
Mar. '79	44.86 \pm 1.10	106.39 \pm 2.08	134.81 \pm 2.88	140.07 \pm 3.77	8.563 \pm 0.159	4.514 \pm 0.165
Apr. '79	63.22 \pm 2.32	92.19 \pm 1.59	170.37 \pm 3.25	175.66 \pm 1.90	8.324 \pm 0.121	5.628 \pm 0.248
May '79	72.47 \pm 0.99	53.92 \pm 2.32	146.67 \pm 2.83	183.70 \pm 3.22	7.929 \pm 0.143	5.441 \pm 0.170
Jun. '79	62.54 \pm 1.58	34.45 \pm 1.68	165.18 \pm 2.14	197.98 \pm 3.46	8.094 \pm 0.145	6.185 \pm 0.092
Jul. '79	56.24 \pm 1.88	48.10 \pm 1.44	152.59 \pm 2.55	165.18 \pm 3.40	6.370 \pm 0.177	7.277 \pm 0.111
Aug. '79	61.60 \pm 2.78	53.89 \pm 2.16	167.41 \pm 2.43	170.37 \pm 3.22	5.605 \pm 0.272	7.441 \pm 0.387
Sep. '79	73.27 \pm 0.64	49.59 \pm 1.96	221.48 \pm 3.57	163.79 \pm 2.78	6.258 \pm 0.102	7.419 \pm 0.219
Oct. '79	74.81 \pm 1.73	44.13 \pm 0.57	183.07 \pm 2.46	151.44 \pm 2.26	6.634 \pm 0.156	7.185 \pm 0.201
Nov. '79	77.87 \pm 2.21	60.44 \pm 1.76	156.30 \pm 2.58	132.59 \pm 2.04	6.817 \pm 0.161	5.889 \pm 0.142
Dec. '79	67.81 \pm 1.47	61.09 \pm 1.84	148.89 \pm 2.34	142.22 \pm 2.67	5.470 \pm 0.157	6.066 \pm 0.276
Jan. '80	78.84 \pm 3.40	70.23 \pm 2.95	167.90 \pm 3.99	161.11 \pm 2.80	6.426 \pm 0.150	6.520 \pm 0.246
Feb. '80	63.98 \pm 1.84	96.30 \pm 1.44	163.79 \pm 1.76	120.00 \pm 2.43	6.668 \pm 0.143	6.318 \pm 0.204
Mar. '80	64.91 \pm 2.32	77.51 \pm 2.50	145.70 \pm 2.22	137.04 \pm 1.91	6.837 \pm 0.158	5.956 \pm 0.245

NS Non-significant. * Significant ($P < 0.05$). ** Highly significant ($P < 0.001$).

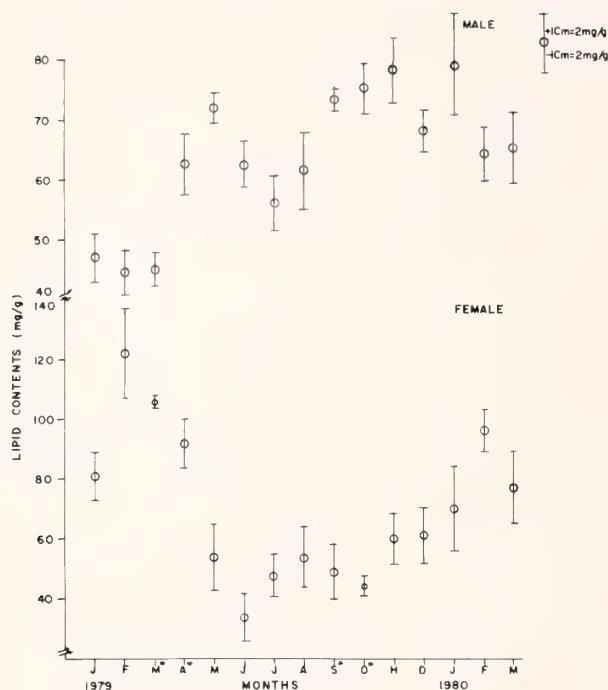


Figure 2

Monthly variations, with standard deviations, in lipid content of soft body tissue of *Viviparus bengalensis*. *Denotes months of intensive breeding activity.

winter months in both the sexes. Similar observations were made by SPECTOR (1956) for clams, oysters, and scallops, and FRAGA (1956) for *Mytilus edulis*. Our results are close to those reported by VENKATARAMAN & CHARI (1951) and DURVE & BAL (1961) for *Ostrea madrasensis*, *Meretrix casta*, and *Crassostrea gryphoides*. However, the difference between the present results and those of LUTGARDS (1950) and ROSAS (1950) may be due to differences in species, environment, geography, and water quality.

Variations in glycogen levels are dependent on feeding and reproductive activities of the snail. The decline in glycogen level in males from January to May and in females from February to July is likely due to its utilization for gametogenesis; peak breeding activity occurs in April. This decline in glycogen level was followed by an increase until August due to postspawning increases in feeding activity. The subsequent decline in September (males) and October (females) is correlated with reproduction: in females, the developing embryos and young consume energy in the form of glycogen. Thereafter, a gradual rise in glycogen level is due to inactivity during hibernation, when catabolic activities are at their lowest. Similar views were expressed by BARRY & MUNDAY (1959), BLACKMORE (1969), WEBBER (1970), and MULEY (1975) concerning similar studies of *Patella vulgata*, *Haliotis cracherodii*, and *Melania scabra*. In the present study, except for January, July, and May, the males had lower glycogen contents than the females. CHATTERJEE & GHOSH (1973) and

LAMBERT & DEHNEL (1974) correlated this higher glycogen in female *Thais lamellosa* with the number of eggs produced, as it provides raw material for their formation. RAO *et al.* (1972) reported very low glycogen contents during aestivation in *Viviparus bengalensis* when low activity levels and decreasing metabolic rates are recorded.

The monthly variations in protein content in the snail had no correlation with the reproductive cycle and might depend upon nutrient conditions and environmental variables. This view was also shared by NAGABHUSHANAM & MANE (1975), but is contrary to that expressed by STICKLE (1975). The results of the present investigation closely resemble those reported by GIESE (1969) for *Tivella stultorum*, but differ from findings of NAGABHUSHANAM & MANE (1975).

In the present study, an increase in lipid content in males from February to May was followed by a decline during spawning months up to July, with another increase until November. The decrease in December was probably due to winter dormancy when there is suspension or reduction in feeding activity, and lipids are consumed for energy. In females, there is a decrease from February to June that is due to lipid utilization for breeding activities, especially the formation of egg capsules in the uterus. From July, lipid levels started increasing during the prespawning period, fell in the spawning months of September and October, and rose again in subsequent months (postspawning period). The lipid values ranged between 3.44 and 12.99% of dry body weight which, according to GIESE (1969) and MULEY (1975), is an appropriate value. In the present investigation, no relationship between sex and the amount of stored fats could be established.

Cholesterol presented a confusing situation. According to VOOGT (1971, 1972) this chemical is the main constituent of lipids in *Viviparus histricus* and other species of *Viviparus*. In the present study, it exhibited a trend independent from that of other lipids. During the major period of study, males exhibited higher values than females. But during the spawning and postspawning months of March to August, females showed higher values than males. The situation was reversed, however, during the second spawning and postspawning stages (September to December) when males exhibited higher values. This suggested that there may be some relationship between cholesterol level and gametogenesis. This, however, requires further investigation.

Because cholesterol was found at high levels and is a principal component of sterols, it could possibly be rich in provitamin D, as suggested by VOOGT (1972) for oysters. As such, it could form a vitamin-D rich food for other animals. This also requires further study to investigate the complex composition of sterols in this snail.

Male snails recorded higher energy values during the spawning months of March–April and September–October, whereas in females, energy values declined during this period. In males, a decreasing pattern of energy values

was witnessed in postspawning months (June to August), whereas in females an increasing trend was shown. In the winter month of December, when all metabolic activities decreased considerably, females recorded higher energy values (6.066 kcal/g) than the males (5.470 kcal/g). The total energy values of *Viviparus bengalensis* suggest high nutritive value of its soft body tissues.

According to GIESE (1969), mollusks lack discrete nutrient storage depots, such as the vertebrate liver, the subdermal and ornamental adipose tissues of mammals, and the fat bodies of lower invertebrates. Thus, nutrient storage occurs primarily through the production of new cellular elements. Seasonal shifts in protein, fats, and glycogen are merely reflections of their relative rates of synthesis and degradation within the body and are often meaningless with respect to seasonal shifts in their contents (STICKLE, 1975). With regard to the biochemical changes in *Viviparus bengalensis*, we conclude that these are related to its reproductive cycles and seasonal environmental variations. This view is in agreement with the findings of MULEY (1975), VENKATARAMAN & CHARI (1951), and DURVE & BAL (1961) for *Melania scabra*, *Ostrea madrasensis*, *Acrosloma variata*, and *Crassostrea gryphoides*. As is apparent from the results of this biochemical analysis, the soft body tissues of *V. bengalensis* have a glycogen economy similar to that of lamellibranchs.

ACKNOWLEDGMENTS

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Gonadal Organization and Gametogenesis in the Fresh-water Mussel *Diplodon chilensis chilensis* (Mollusca: Bivalvia)

by

SANTIAGO PEREDO AND ESPERANZA PARADA

Department of Natural Sciences, Catholic University of Chile-Temuco,
Casilla 15-D, Temuco, Chile

Abstract. The gonadal organization and cytological characteristics of gametogenesis in the fresh-water mussel *Diplodon chilensis chilensis* are described. Although the sexes did not differ macroscopically, gonadal sections demonstrate the existence of gonochoric individuals in which testis and ovary are clearly distinct. In both sexes, gonads are ramified organs bearing numerous follicles closely packed among the intestine coils. Follicles in males contain gametes at different stages of maturation which can be recognized by their shape, size, and nuclear features. They are organized in clusters of spermatogonia, primary and secondary spermatocytes, and spermatids. Spermatozoa are accumulated in the lumen of follicles. Follicles of the female gonad contain oogonia and oocytes at different stages of development. Morphological features similar to those described in other fresh-water and marine bivalves are apparent. In the specimens of the size classes examined, no differences in the gonadal organization and gametogenesis were observed during the study period.

INTRODUCTION

DUE TO CHILE's extensive coastline (approximately 4200 km) and the subsequent diversity and abundance of marine invertebrates, most of the studies about reproduction and other aspects of the biology of mollusks have been carried out on marine species, especially those of commercial value. A review of the literature shows that many aspects of the biology of the fresh-water mollusks inhabiting Chile have never been studied. Practically nothing is known about the reproduction of the fresh-water mussel *Diplodon chilensis chilensis* (Gray, 1828) although it is abundant in rivers and lakes of Chile and ranges from Arica in the North (18°30') to the Strait of Magellan in the southern part of the country (53°). *Diplodon chilensis chilensis* is a hardy bivalve that tolerates temperature and oxygen level changes and possesses a high filtration capacity (BUSSE, 1970).

Due to the vulnerability of the gonadic tissue to environmental contaminants such as organochlorine compounds, pesticides, and heavy metals, the study of the reproduction of *Diplodon chilensis chilensis* is of importance in biological monitoring studies. This species may prove useful as an indicator of environmental changes due to fresh-water pollution, which in turn may be a source of pollution of coastal waters. The subsequent negative ef-

fects of such pollutants on littoral communities have been reported in several studies (KNAUER & MARTIN, 1972; WILLIAMS & WEISS, 1973; BERGE & HILLEBRAND, 1974; WOLF, 1975; REIJNDERS, 1980).

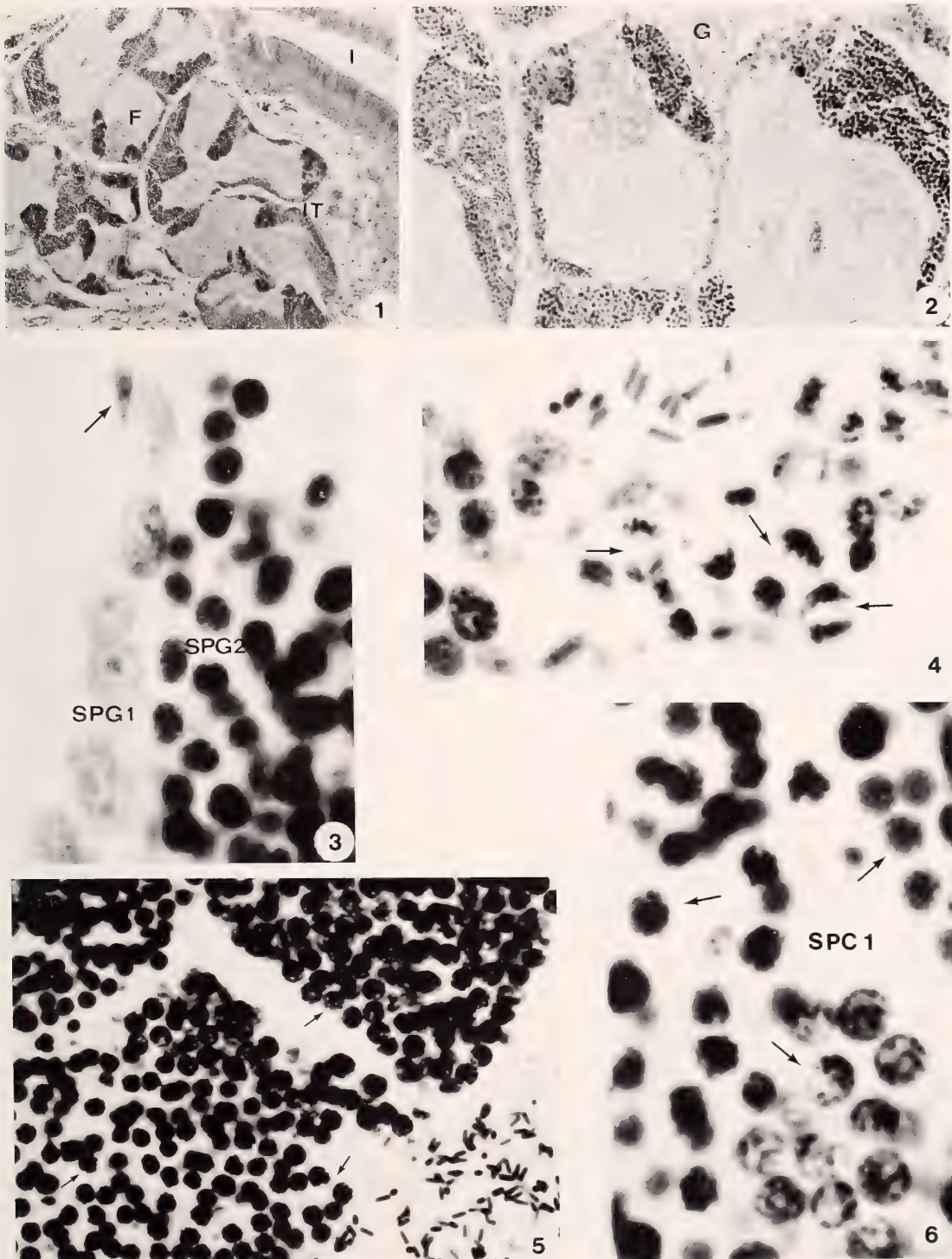
The present study analyzes the histology of the gonads and the cytological characteristics of gametogenesis in *Diplodon chilensis chilensis*.

MATERIALS AND METHODS

In March 1982, specimens of *Diplodon chilensis chilensis* were collected at random from shallow waters of Lake Villarrica (39°17'S, 72°13'W). The mussels lived at depths ranging from 20 to 60 cm. The individuals were distributed in eight sizes grouped in the following classes: S₁ (16-25 mm); S₂ (26-30 mm); S₃ (31-35 mm); S₄ (36-40 mm); S₅ (41-45 mm); S₆ (46-50 mm); S₇ (51-55 mm); and S₈ (56-65 mm).

Five individuals were selected at random from each size class. The sex was determined by gonad smears. The viscera were fixed in aqueous Bouin's fixative. After embedding in paraffin, serial sections were cut at 7 µm and stained with hematoxylin and eosin.

The gonadal organization and the cytological characteristics of the germinal and somatic cells of both sexes were inspected using a light microscope.



Explanation of Figures 1 to 6

Figure 1. A topographical view of the male gonad of *Diplodon chilensis chilensis*. The well delimited follicles (F) occupy the visceral mass (mesosoma) surrounding the intestine (I). Scanty interstitial tissue (IT) is present among follicles. $\times 20$.

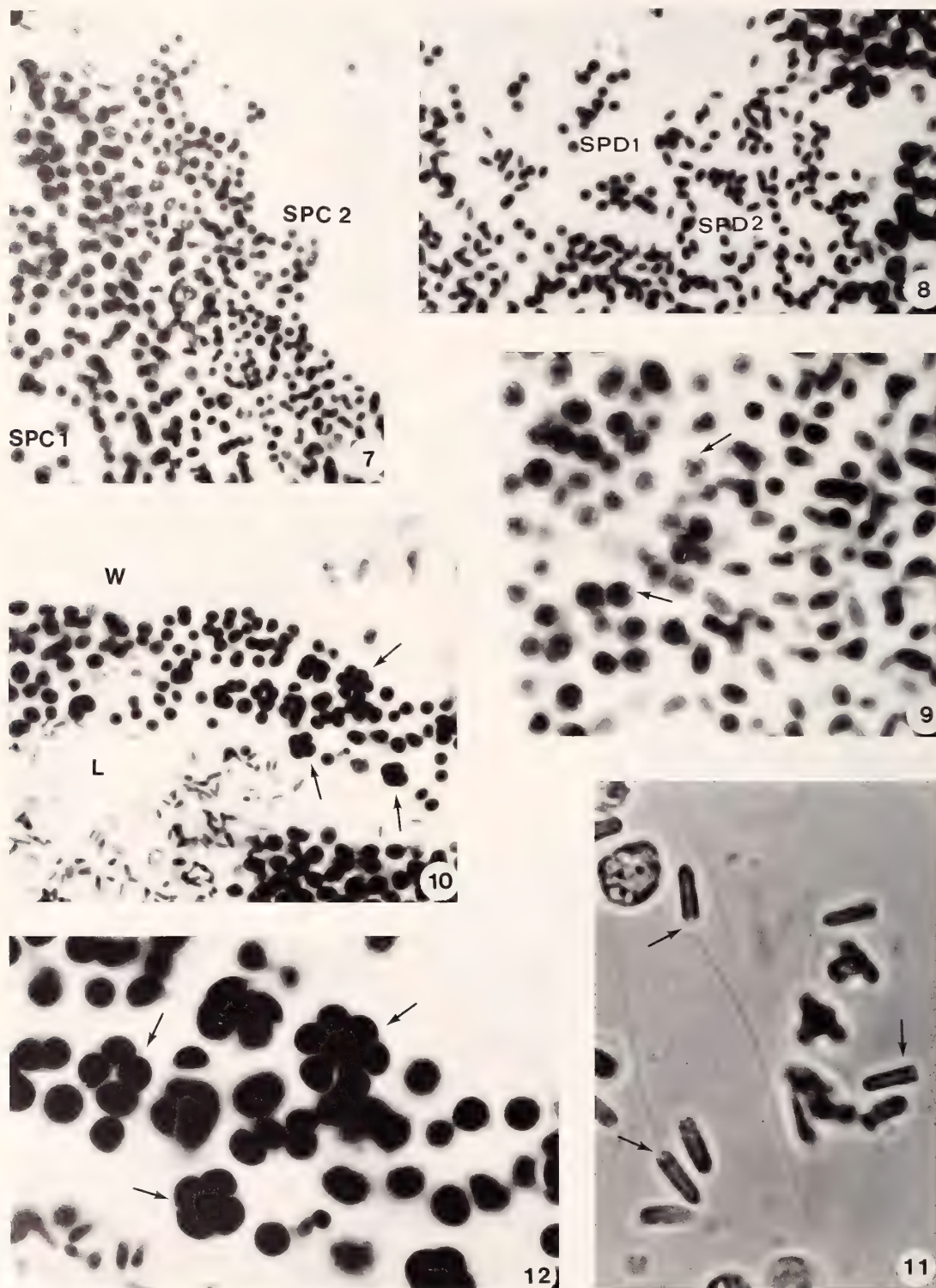
Figure 2. Cell clusters within follicles. A gonoduct (G) is seen next to the follicles. $\times 50$.

Figure 3. Type 1 spermatogonia (SPG 1) in single rows and

type 2 spermatogonia (SPG 2) in clusters in a follicle. The spindle-shaped nucleus (arrow) is from a cell of the follicle wall. $\times 500$.

Figure 4. Type 1 spermatogonia showing some mitotic figures (arrows). $\times 500$.

Figures 5, 6. Clusters of primary spermatocytes (SPC 1) showing meiotic prophase configurations (arrows). $\times 200$, $\times 500$.



Explanation of Figures 7 to 12

Figure 7. Clusters of secondary spermatocytes (SPC 2) interspersed with spermatids with rounded nuclei. The nuclei of these cell types are hardly distinguishable. Next to them are primary spermatocyte nuclei (SPC 1). $\times 200$.

Figures 8, 9. Clusters of spermatids with rounded nuclei (SPD 1) and elongate nuclei (SPD 2). The acrosomal vacuole can be seen (arrows). $\times 200$, $\times 500$.

RESULTS

Diplodon chilensis chilensis is dioecious, as are the great majority of bivalves, and sexual dimorphism is absent.

Male Gonad and Germ Cells

The male gonad consists of numerous follicles located in the visceral mass surrounding the intestinal coils. The follicles show diversity in shape and size and are delimited by a thin cellular enveloping membrane (Ancel's layer) which may have some connective fibers applied to it. Scanty interstitial (connective) tissue surrounds the follicles (Figure 1).

The follicles are crowded with cells at different stages of spermatogenesis. The cells of particular stages can be recognized by their shape, size, and nuclear features, and are arranged in groups or clusters markedly delimited and located at the periphery of the follicles (Figure 2).

The gonoducts are branched and smaller in diameter than follicles; a lumen is always present. The walls are lined with a single row of ciliated columnar cells with elliptical nuclei. The cytoplasm stains lightly with eosin (Figure 2).

Spermatogonia: Two types of spermatogonia can be recognized. Those of the first type are less numerous than the second and lie in a single row against the membrane enveloping the follicles. These spermatogonia have large vesicular nuclei (9.0–10 μm) with a conspicuous nucleolus and loose chromatin (Figure 3). Fibroblast-like cells are seen next to this type of spermatogonia. The fibroblast-like cells are in the follicle wall. Their nuclei are spindle shaped, and the cytoplasm is difficult to visualize (Figure 3). The second type of spermatogonia occurs in clusters without visible cytoplasm and lies close to, or sometimes interspersed with, primary spermatocytes. The densely reticulate nuclei possess no nucleoli and are smaller and stain more heavily than the first type of spermatogonia (Figure 3). Occasionally, mitotic figures can be seen in the first type of spermatogonia (Figure 4).

Primary spermatocytes: These cells form numerous and compact clusters. They have a fine, faintly staining plasma membrane and a clear, scanty cytoplasm, but these features are barely visible in the congested mass of nuclei. The nuclei vary in appearance as the chromatin assumes different consistencies and locations within the nucleus. The chromosomes can be scattered in the nucleus or they may be polarized at the periphery showing typical figures of meiotic prophase (Figures 5, 6).

Secondary spermatocytes: Secondary spermatocytes are seen less commonly than primary spermatocytes. They

occur in groups generally intermingled with spermatids forming mixed cell groups (Figure 7). Secondary spermatocytes have small, round nuclei (3.0 μm) with granular and heavily staining chromatin.

Spermatids: The nucleus of one type of spermatid is similar in shape, size, and staining properties to that of the secondary spermatocytes (Figure 8). A second type of nucleus can be seen in the spermatid groups. These nuclei are elongate, stain heavily and homogeneously, and have a short eosinophilic zone at one end (Figures 8, 9). They are intermingled with the nuclei of the first type of spermatid which show a vacuole similar to the acrosomal granule (Figure 9).

Spermatozoa: Spermatozoa are formed in the center of the follicles where they accumulate. The mature spermatozoon has an elongate head about 4.0 μm long and 1.5 μm wide. The chromatin is dense and stains homogeneously (Figure 10). Fresh smears of gonad tissue show flagella four to five times the length of the heads (20–24 μm) emerging from the eosinophilic mass at one end of the sperm heads (Figure 11).

In addition to normal germinal cells, the follicles of many males also contain numerous multinucleated spherical dark bodies (Figure 12) similar to those described in *Mya arenaria* (COE & TURNER, 1938; SHAW, 1965; PORTER, 1974) and *Cyprina islandica* (LOOSANOFF, 1953). Such dark bodies are usually closer to the periphery of the follicles than to their center, and contain a variable number of pycnotic nuclei (from 2 to 10 nuclei); alternatively, they can be seen as single nuclei (Figure 12).

Female Gonad and Germ Cells

As in males, the female gonad of *Diplodon chilensis chilensis* is a branched gland embedded in the visceral mass. Numerous follicles surround the coils of the intestine (Figure 13). The follicles are irregular in size and shape, and are limited by a connective tissue wall of variable thickness.

In the follicles, germ cells at different stages of development can be recognized by their size, shape, and staining properties (Figure 13).

Oogonia: Oogonia are observed embedded in the follicle walls. They are distinguished from the connective tissue cells by their relatively large size and highly chromatic nuclei (Figures 14, 15).

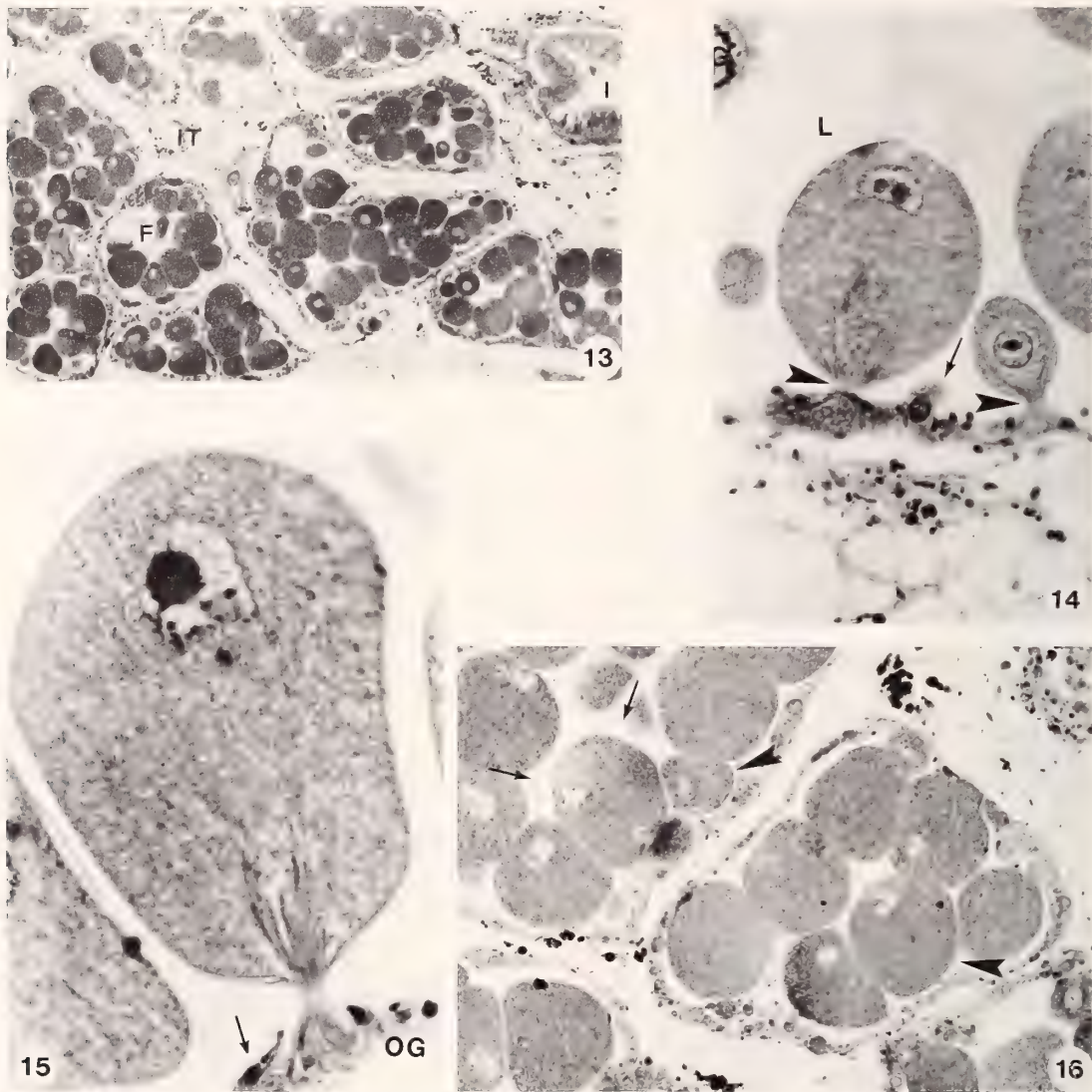
Growing oocytes—previtellogenic oocytes: The shape of the newly formed oocytes may be square, cylindrical, or hemispherical (Figures 13, 14). They bulge from the

Figure 10. Sperm in the lumen of a follicle (L). Next to the wall (W) lie multinucleated spherical bodies (arrows) of atypical spermatogenesis. $\times 200$.

Figure 11. Gonad smear with spermatozoa. The flagellum can

be seen emerging from the eosinophilic end of the sperm head (midpiece) (arrows). $\times 500$.

Figure 12. Multinucleated spherical bodies (atypical spermatogenesis). $\times 500$.



Explanation of Figures 13 to 16

Figure 13. Topographical view of the female gonad of *Diplodon chilensis chilensis*. The follicles (F) in the visceral mass surround the intestine (I). Scanty interstitial tissue (IT) is present among follicles. $\times 20$.

Figure 14. Previtellogenic oocyte bulging from the follicle wall (arrow). Protruding into the lumen (L) growing oocytes can be seen attached by a cytoplasmic stalk (arrow head). $\times 500$.

Figure 15. Growing (vitellogenic) oocyte with slender stalk. Oogonium (OG) and wall cell nuclei (arrow) embedded in the follicle wall. $\times 500$.

Figure 16. Full grown oocytes in follicles. The vitelline membrane is sloughed away in some (arrows). Growing oocytes (arrow heads). A gonoduct can be seen. $\times 500$.

follicle wall, and the largest ones are attached to the follicle wall by a short, broad stalk (Figure 14). The cytoplasm is basophilic and the nucleus is large, stains lightly, and has disperse chromatin with one or two prominent basophilic or eosinophilic nucleoli (Figure 14).

Growing oocytes—vitellogenic oocytes: As the oocytes grow they elongate and protrude into the center of the follicles. The nucleus migrates to the distal or free end of the cell (Figures 14, 15). The stalk becomes thinner and

the oocytes increase in size as yolk accumulates. Bundles of fibrillar material can be seen in the stalk and in the cytoplasm close to the stalk (Figure 15). The nucleus enlarges and stains less heavily as the chromatin disperses. The nucleoli continue to grow and in some oocytes are seen to be eosinophilic or basophilic.

Full grown oocytes (morphologically mature): These oocytes have become freed from the follicle wall and have moved into the lumen. They are more regular in outline

than the attached oocytes, and they are larger than vitellogenic oocytes, even though some of the latter can reach a larger size than the free ones. Full grown oocytes can reach up to 150 μm in diameter. The germinal vesicle is intact and lightly stained, with dispersed chromatin; the nucleoli are prominent. The cytoplasm is loaded with vitelline platelets (Figure 16).

One can see in developed oocytes (growing and full grown oocytes) a covering, the vitelline membrane, which is rather thick and prominent close to the cytoplasmic stalk in attached oocytes (Figures 15, 16).

The interstitial tissue consists of vesicular connective tissue in which are abundant cells similar to those called Cell Type A by TRANTER (1958) although they were not seen within the follicles in the present study. These cells are especially abundant in the tissue surrounding the intestine (Figure 13).

The gonoducts show the same features described for the gonoducts of the male gonad (Figures 14, 16).

DISCUSSION

The structure of the gonad of *Diplodon chilensis chilensis* corresponds largely to that described for the fresh-water mussels *Anodonta cygnea* (PURCHON, 1968), *Sphaerium simile* (GILMORE, 1917), *Lamellidens corrianus* (NAGABHUSHANAM & LOHGAONKER, 1978), and some marine bivalves, in which the gonad is a branched gland that terminates in a network of follicles occupying a large part of the visceral mass. A system of branched ducts, the gonoducts, evacuate ripe germ cells during spawning periods. *Diplodon ch. chilensis* differs from other bivalves, such as *Mytilus edulis*, in which the gonad penetrates into mantle tissue (SASTRY, 1977). Copulatory organs and accessory glands are absent.

Although macroscopic sexual dimorphism is not present, microscopic observations show that *Diplodon ch. chilensis* is strictly gonochoric, because even in the smallest specimens sampled (16 mm) only male or female follicles could be recognized in the same individual.

Male germ cells correspond with the usual types formed during spermatogenesis. No indifferent or primordial germ cells, described for some pelecypods (TRANTER, 1958; LUBET, 1959), were recognized in *Diplodon ch. chilensis*. At least two types of spermatogonia can be recognized. The first type (type 1 spermatogonia) would be primitive spermatogonia, less advanced than the second type recognized (type 2 spermatogonia) which would be definitive spermatogonia since these are the end products of spermatogonial mitosis. Type 2 spermatogonia directly give rise to primary spermatocytes.

The variable appearance of the nuclei of primary spermatocytes corresponds to the various configurations of meiotic prophase (Figures 5, 6). Primary spermatocytes give rise to secondary spermatocytes. These are seen less commonly than their predecessors. Apparently, division is very rapid at this stage, with the secondary spermatocytes

giving rise to the first type of spermatid characterized by the nuclear vacuole, which would correspond to the onset of the acrosomal granule formation. Spermatids with elongated nuclei are cells in advanced stages of differentiation into spermatozoa.

The eosinophilic zone described in one of the ends of the sperm head corresponds to the midpiece of the spermatozoa and possibly consists of an aggregate of mitochondria as described in *Haliotis rufescens* (YOUNG & DE MARTINI, 1970). This view is supported by the examination of fresh smears in which the flagellum is seen emerging from the eosinophilic mass (Figure 11).

The multinucleated spherical dark bodies observed in the follicles of many males (Figures 10, 12) would be cells of atypical spermatogenesis according to LOOSANOFF (1953) who described them in the spermatogenesis of *Cyprina islandica* and earlier in *Mercenaria mercenaria* (LOOSANOFF, 1937a). They have also been described in *Mya arenaria* (COE & TURNER, 1938; SHAW, 1965; PORTER, 1974) as well as in the unionids *Anodonta anatina* (BLOOMER, 1936), *A. cygnea* (BLOOMER, 1946), and *A. grandis* (VAN DER SCHALIE & LOCKE, 1941). According to HEARD (1975) these abnormal cells are of widespread occurrence in the Unionacea, having been found in 43 species of 17 genera in the families Amblemidae, Hyriidae, Margaritiferidae, and Unionidae. COE & TURNER (1938) point out that in some cases such multinucleated dark bodies may break apart and continue further development, finally reaching the stage of spermatozoa. BLOOMER (1946) inferred that in *A. cygnea* these atypical cells (sperm-morulae) metamorphosed into mature spermatozoa based on the observed disappearance of sperm morulae just prior to the appearance of large numbers of spermatozoa. More often they become pycnotic and are cytolized. The observations made in the present study do not elucidate the ultimate fate of these abnormal cells.

Oogenesis in *Diplodon ch. chilensis* has the usual characteristics described for other fresh-water and marine mollusks. Growing oocytes with a cytoplasmic stalk have also been described for *Anodonta* (BEAMS & SEKHON, 1966), *Sphaerium simile* (ZUMOFF, 1973), and in several Chilean marine bivalves (CIFUENTES, 1975; LOZADA & REYES, 1981). In gastropods, HUAQUÍN (1979) described previtellogenic oocytes attached by a stalk to the germinative epithelium of the ovary in *Concholepas concholepas*, and a similar situation was described for *Haliotis rufescens* (YOUNG & DE MARTINI, 1970). BEAMS & SEKHON (1966) described abundant and closely packed microtubules in the stalks of developing oocytes. These authors assign a mechanical and also a possible nutritional role for these microtubules in the growing oocyte.

The observations made in the above-mentioned several species and those made in the present study indicate that oocytes apparently remain attached by means of the cytoplasmic stalk to the ovarian wall during much of their development. In *Diplodon ch. chilensis* oocytes up to 120 μm in diameter could be seen to be connected to the fol-

lucular wall, although it was not possible to determine exactly when they became detached.

An intact germinal vesicle in full grown oocytes indicates that they are not physiologically mature. In these oocytes meiosis either may be arrested at early prophase, in the vegetative phase (RAVEN, 1966), or meiosis may not have started yet, as has been reported for other bivalves (LOOSANOFF, 1937a, b; 1953). Therefore, in *Diplodon ch. chilensis* either the germinal vesicle would initiate maturation just before spawning, or eggs are released with the nucleus intact and the initiation of meiosis would occur after the sperm has penetrated the egg (activation), as has been reported for other fresh-water bivalves (OKADA, 1935; ZUMOFF, 1973) and marine mollusks (BRETSCHNEIDER & RAVEN, 1951; GALSTOFF, 1961; STICKNEY, 1963). LILLIE (1901) reported that in the unionid *Elliptio complanatus* diploid primary oocytes and not mature haploid ova were released from the ovaries and the reduction division of these cells did not occur until after sperm penetration (in the marsupial demibranchs).

The rather thick vitelline membrane that covers oocytes of *Diplodon ch. chilensis* is characteristic of many fresh-water bivalves (FRETTER & GRAHAM, 1964). No evidence of a second cover, the chorion, as described for several bivalves including the fresh-water mussel *Anodonta* (BEAMS & SEKHON, 1966), have been found in *Diplodon ch. chilensis*.

The meaning and significance of interstitial cells seen in males and females of *Diplodon ch. chilensis* is not clear. LOOSANOFF (1937a, b) assigns to cells of the surrounding connective tissue (amoebocytes) a nutritional role in the active phase of the reproductive cycle of *Mercenaria mercenaria*. TRANTER (1958) ascribes to these cells a resorptive function in follicles emptied from gametes after spawning and during early development in *Pinctada albina*. No evidence for any of these roles could be obtained in the present study since interstitial cells were always seen outside the follicles and with no connection to the germinal cells.

There was no observed difference in gametogenesis in different size classes. *Diplodon ch. chilensis* reaches sexual maturity at a size smaller than 16 mm, the size of the smallest specimens analyzed in this study.

ACKNOWLEDGMENTS

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The Effects of Aerial Exposure and Desiccation on the Oxygen Consumption of Intertidal Limpets

by

ALASTAIR J. INNES¹

Portobello Marine Laboratory, University of Otago,
Dunedin, New Zealand

Abstract. Aquatic and aerial rates of oxygen consumption were determined for the intertidal prosobranch limpets *Notoacmea pileopsis* and *Cellana radians* at 10°C. Rates of oxygen consumption of the two species did not differ significantly between aquatic and aerial environments. The aerial rates of oxygen uptake of both species decreased significantly after a period of desiccation. The results are discussed with reference to previous reports on the respiration of acmaeid and patellid limpets in air and water.

INTRODUCTION

A FEATURE of the rocky shores of New Zealand is the presence of an acmaeid limpet, *Notoacmea pileopsis* (Hombron & Jacquinot, 1841), in the splash zone (MORTON & MILLER, 1968). Acmaeid limpets retain a primitive aspidobranch gill (PURCHON, 1968) and are more frequently encountered in low shore or subtidal habitats. Previous respiratory studies on intertidal and subtidal acmaeids have reported depressed rates of oxygen consumption during aerial exposure (BALDWIN, 1968; MCMAHON & RUSSELL-HUNTER, 1977). In contrast, patellid limpets, which possess secondary pallial gills, are often found on the upper levels of the shore, and several species appear capable of maintaining aerobic metabolism during emersion (BANNISTER, 1974; BRANCH & NEWELL, 1978; HOULIHAN & NEWTON, 1978; BRANCH, 1979). In the present study, the oxygen consumption of *Notoacmea pileopsis* in water and air is investigated to determine whether this limpet's vertical distribution on the shore is correlated with an enhanced capacity for aerial gas exchange as has been demonstrated for other gastropods (MICALLEF, 1967; MICALLEF & BANNISTER, 1967; MCMAHON & RUSSELL-HUNTER, 1977; HOULIHAN, 1979; HOULIHAN & INNES, 1982a, b). The relationship between aquatic and aerial oxygen uptake is also determined for a common intertidal patellid limpet, *Cellana radians* (Gmelin, 1791), from the same shore. The relative ability of acmaeid and patellid limpets to respire in aquatic and aerial environ-

ments is discussed with respect to their principal organs of gas exchange (MCMAHON & RUSSELL-HUNTER, 1977).

BALDWIN (1968) demonstrated that the aerial oxygen consumption of acmaeid limpets is significantly depressed after a period of desiccation, but no comparable data are available for patellid limpets. In the present study the effects of desiccation on the aerial rates of oxygen consumption of both *Notoacmea pileopsis* and *Cellana radians* have been investigated and the results are discussed in relation to the respiratory structures of each species. Comparisons are made with a number of other intertidal prosobranchs (SANDISON, 1966; BALDWIN, 1968; SHIRLEY *et al.*, 1978).

MATERIALS AND METHODS

This work was carried out at the Portobello Marine Laboratory, New Zealand, between August and October 1982. The prosobranchs investigated in the present study are the acmaeid limpet *Notoacmea pileopsis*, which is distributed in the splash zone, and the patellid limpet *Cellana radians*, which is commonly found in the intertidal zone (MORTON & MILLER, 1968; POWELL, 1979). All experimental animals were collected from Allans Beach, Portobello.

After collection, the snails were held in a running seawater aquarium without access to food for 7 to 9 days prior to experimentation. The aquarium seawater temperature varied between 7 and 10°C and the salinity was relatively constant at 33.5‰. Experiments were carried out at 10°C and the snails were held at the experimental temperature for two hours prior to respirometry commencing. Experiments took place in constant temperature water baths controlled to $\pm 0.1^\circ\text{C}$.

Aerial rates of oxygen consumption were measured us-

¹ Current mailing address: Department of Zoology, University of the West Indies, St. Augustine, Trinidad, West Indies.

ing constant pressure respirometers described by DAVIES (1966). The limpets were allowed to recover extra-corporeal fluid as described by HOULIHAN & NEWTON (1978) prior to experiments commencing. For desiccation experiments the respirometer bottles containing the snails were placed in desiccation chambers and held in a constant temperature room at 10°C for periods of 1, 4, and 8 h. Silica gel was used as a desiccating agent and relative humidity (RH) was constant at 20%. Aerial respirometry was carried out as described by HOULIHAN *et al.* (1981). The position of the snail in the respirometer was monitored and rates of oxygen consumption calculated for periods when the animal was seen to be inactive. All rates of oxygen consumption have been converted to STP. Some determinations of aerial oxygen consumption for *Notoacmea* were made with up to three similar-sized snails in a respirometer in order to increase the accuracy of the measurements. These data are expressed as mean oxygen consumption for a mean weight animal.

Aquatic oxygen consumption was measured by the closed bottle technique described by HOULIHAN (1979). The limpets were left overnight to attach and settle in the respirometer bottles in running aerated seawater prior to experiments commencing (HOULIHAN & NEWTON, 1978). After the flasks were sealed, the seawater was stirred every 5 min with a magnetic stirrer, and rates of oxygen consumption were calculated only for those animals that remained inactive throughout the experiment. A blank bottle without an animal was run as a control with each set of experiments. The oxygen content of the seawater at the beginning and end of each experiment was determined by the Winkler technique (STRICKLAND & PARSONS, 1972). Oxygen consumption was calculated from the decline in oxygen content of the seawater, the volume of water in the respirometer bottle, and the duration of the experiment. The oxygen content of the seawater in the flask was never allowed to fall below 80% of the saturated value during experiments (INNES, 1982).

At the end of each experiment the limpets were removed from their shells and dried to a constant weight at 65°C.

Measurements of aquatic and aerial (undesiccated) respiration were made on a wide size range of animals in order to establish relationships between dry weight and oxygen consumption. The results were subjected to regression and covariance analysis (SNEDECOR & COCHRAN, 1972) following the procedure of WILSON (1975). The results of regression analysis using data transformed by logarithms to the base 10 are shown in their logarithmic form. The mean dry flesh weight \pm SE of all the *Notoacmea pileopsis* used in these experiments was 42.5 ± 2.5 mg ($n = 46$) while that of the larger *Cellana radians* was 219.6 ± 24.2 mg ($n = 41$). Standard dry flesh weight animals, *Notacmea pileopsis* (40 mg) and *Cellana radians* (200 mg), were used to calculate ratios of aquatic to aerial oxygen consumption and to describe the effects of desiccation.

Narrow weight ranges of *Notoacmea pileopsis* (30–50

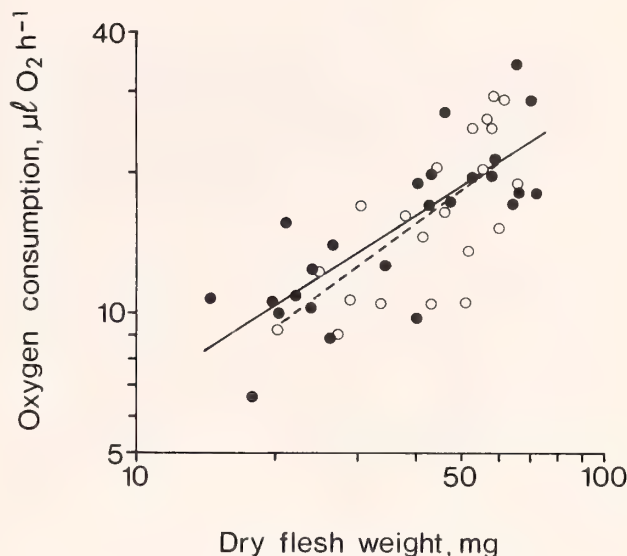


Figure 1

Relationships between dry flesh weight (mg) and oxygen consumption ($\mu\text{L O}_2 \text{ h}^{-1}$) of *Notoacmea pileopsis* in air (○—○) and seawater (●—●) at 10°C; the lines are drawn from the regression analyses provided in the text.

mg) and *Cellana radians* (160–240 mg) were selected for desiccation experiments. The experimentally determined rates of oxygen consumption of individual animals were transformed to those of standard dry weight *Notoacmea* (40 mg) and *Cellana* (200 mg) using the scaling equation:

$$\dot{V}_{\text{O}_2}(\text{s}) = \left(\frac{W(\text{e})}{W(\text{s})} \right)^b \cdot \dot{V}_{\text{O}_2}(\text{e})$$

(NEWELL, 1979)

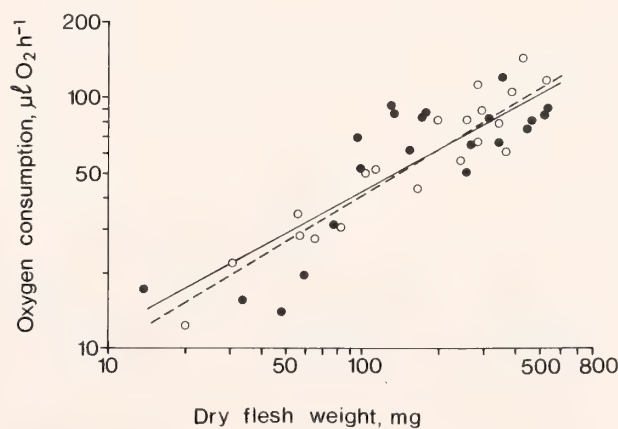


Figure 2

Relationships between dry flesh weight (mg) and oxygen consumption ($\mu\text{L O}_2 \text{ h}^{-1}$) of *Cellana radians* in air (○—○) and seawater (●—●) at 10°C; the lines are drawn from the regression analyses supplied in the text.

Table 1

Ratios of aquatic oxygen consumption for a number of acmaeid and patellid limpets; ratios have been calculated at the temperatures indicated for standard weight animals using data supplied in the references.

Species	Tem- pera- ture (°C)	Aquatic to aerial ratio	Reference
Acmaeidae:			
<i>Notoacmea pileopsis</i>	10	1:0.95	present study
<i>Collisella scabra</i>	15	1:0.44	BALDWIN (1968)
<i>Collisella digitalis</i>	15	1:0.89	BALDWIN (1968)
<i>Collisella testudinalis</i>	22	1:0.40	McMAHON & RUSSELL-HUNTER (1977)
Patellidae:			
<i>Cellana radians</i>	10	1:0.97	present study
<i>Patella lusitanica</i>	20	1:3.13	BANNISTER (1974)
<i>Patella caerulea</i>	20	1:0.45	BANNISTER (1974)
<i>Patella oculus</i>	25	1:0.99	BRANCH & NEWELL (1978)
<i>Patella cochlear</i>	25	1:1.04	BRANCH & NEWELL (1978)
<i>Patella granularis</i>	25	1:0.94	BRANCH & NEWELL (1978)
<i>Patella vulgata</i>	10	1:1.41	HOULIHAN & NEWTON (1978)
<i>Patella granatina</i>	25	1:0.99	BRANCH (1979)

where $\dot{V}_{O_2}(s)$ is the calculated rate of oxygen consumption of a standard dry weight animal in $\mu\text{L O}_2 \text{ h}^{-1}$; $W(s)$, the dry flesh weight of a standard animal in mg; $W(e)$, the dry flesh weight of the experimental animal in mg; $\dot{V}_{O_2}(e)$, the experimentally determined oxygen consumption in $\mu\text{L O}_2 \text{ h}^{-1}$; b , the scaling exponent (aerial b values of 0.717 and 0.645 determined for *Notoacmea* and *Cellana* respectively in the present study are used). Statistical comparisons between rates of oxygen consumption under different experimental conditions were made by Students t -test (SNEDECOR & COCHRAN, 1972). Means \pm SE are used throughout.

RESULTS

Oxygen Consumption in Air and Seawater

Rates of oxygen consumption in air and water of a size range of *Notoacmea pileopsis* are presented in Figure 1. The regression analyses describing the relationships between dry flesh weight (X , mg) and oxygen consumption (Y , $\mu\text{L O}_2 \text{ h}^{-1}$) are

$$\text{Air} \quad \log_{10} Y = 0.717 \log_{10} X + 0.036, \text{ where } n = 21 \text{ and } r = 0.71.$$

$$\text{Seawater} \quad \log_{10} Y = 0.643 \log_{10} X + 0.176, \text{ where } n = 25 \text{ and } r = 0.80.$$

The relationships between dry flesh weight and oxygen

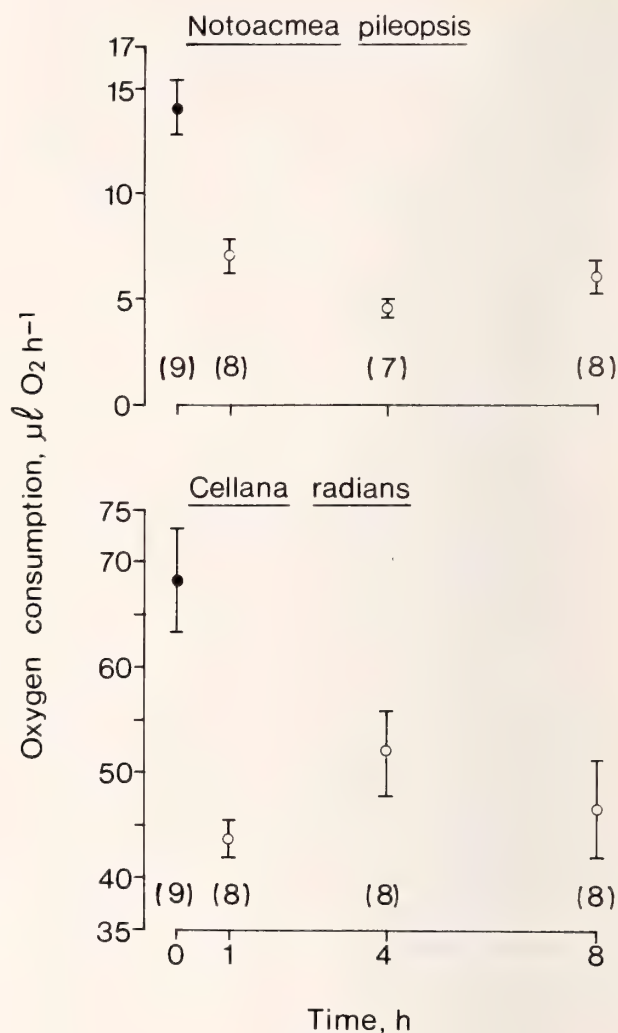


Figure 3

Rates of aerial oxygen consumption ($\mu\text{L O}_2 \text{ h}^{-1}$) \pm SE of standard dry weight *Notoacmea pileopsis* (40 mg) and *Cellana radians* (200 mg) after a brief period of aerial exposure (\bullet) and after 1 h, 4 h, and 8 h desiccation at 20% RH (\circ); sample sizes (n) are shown in parentheses.

consumption in air and water are both significant ($P < 0.05$). Analysis of covariance showed no significant differences in either slope or elevation between the rates of oxygen consumption of *Notoacmea pileopsis* in aquatic and aerial environments. The ratio of aquatic to aerial oxygen consumption for a standard dry weight animal (40 mg) is 1:0.95 at 10°C.

Aquatic and aerial rates of oxygen consumption of *Cellana radians* are plotted as a function of dry flesh weight in Figure 2. The relationships between dry flesh weight (X , mg) and oxygen consumption (Y , $\mu\text{L O}_2 \text{ h}^{-1}$) are described by the regression analyses

$$\text{Air} \quad \log_{10} Y = 0.645 \log_{10} X + 0.323, \text{ where } n = 20 \text{ and } r = 0.94.$$

Table 2

Ratios of the aerial oxygen consumption of gastropods soon after emersion to that of animals subjected to a period of desiccation; ratios for the species in the present study are calculated after 4 h desiccation (20% RH) at 10°C for comparison with those reported by SANDISON (1966) after 3 h drying at 18°C and by BALDWIN (1968) after 3 h drying at 22°C; the principal respiratory organ of each species is indicated; NS denotes no significant difference between desiccated (after drying overnight) and undesiccated rate.

Species	Principal respiratory organ	Ratio of oxygen consumption	Reference
<i>Notoacmea pileopsis</i>	bipectinate gill	1:0.32	present study
<i>Collisella scabra</i>	bipectinate gill	1:0.43	BALDWIN (1968)
<i>Collisella digitalis</i>	bipectinate gill	1:0.25	BALDWIN (1968)
<i>Cellana radians</i>	pallial gills	1:0.76	present study
<i>Littorina saxatilis</i>	unipectinate gill	1:0.72	SANDISON (1966)
<i>Littorina littorea</i>	unipectinate gill	1:0.40	SANDISON (1966)
<i>Littorina obtusata</i>	unipectinate gill	1:0.38	SANDISON (1966)
<i>Nucella lapillus</i>	unipectinate gill	1:0.52	SANDISON (1966)
<i>Littorina irrorata</i>	unipectinate gill	NS	SHIRLEY <i>et al.</i> (1978)

Seawater $\log_{10} Y = 0.559 \log_{10} X + 0.511$, where $n = 21$ and $r = 0.83$.

The correlation coefficients for the aerial and aquatic regression analyses are both significant ($P < 0.05$). Analysis of covariance revealed no significant differences in either slope or elevation between the rates of oxygen consumption determined in air and seawater. The aquatic to aerial ratio for a standard weight animal (200 mg) is 1:0.97 at 10°C.

Effect of Desiccation on Aerial Oxygen Consumption

Aerial rates of oxygen consumption of *Notoacmea pileopsis* after 1, 4, and 8 h desiccation are all significantly lower ($P < 0.001$) than rates determined for limpets that had experienced a brief period of aerial exposure (Figure 3). The rates measured after 1 and 4 h desiccation are also significantly different ($P < 0.05$). The aerial oxygen consumption of *Notoacmea* decreases by over 50% at all three levels of desiccation—1 h (51%), 4 h (68%), and 8 h (57%).

The aerial oxygen consumption of *Cellana radians* decreases significantly after 1 h ($P < 0.001$), 4 h ($P < 0.05$), and 8 h ($P < 0.01$) desiccation compared to limpets after a brief period of aerial exposure (Figure 3). There are no significant differences between the rates after 1, 4, and 8 h desiccation. Decreases in the aerial oxygen consumption of *Cellana radians* after 1 h (36%), 4 h (24%), and 8 h (32%) desiccation are less than those reported for *Notoacmea pileopsis*.

DISCUSSION

In terms of its respiration in air and water, the acmaeid limpet *Notoacmea pileopsis* is an exception to the pattern of depressed rates of aerial oxygen consumption previously described for prosobranch limpets possessing primitive aspidobranch gills (BALDWIN, 1968; HUGHES, 1971a;

McMAHON & RUSSELL-HUNTER, 1977). The distribution of *Notoacmea pileopsis* may be compared with that of some neritids (HUGHES, 1971b; LEWIS, 1971; COLEMAN, 1976; HOULIHAN, 1979) and trochids (MICALLEF, 1967; MICALLEF & BANNISTER, 1967; HOULIHAN & INNES, 1982a, b) which also retain a bipectinate ctenidium and are subjected to long periods of aerial exposure.

The pattern of respiration in air and water for a number of acmaeid limpets (Table 1) seems somewhat similar to that described in comparative studies of trochids (MICALLEF, 1967; MICALLEF & BANNISTER, 1967; HOULIHAN & INNES, 1982a, b), *i.e.*, high shore species maintain aerobic metabolism during emersion while their low shore counterparts have reduced rates of oxygen consumption in air. Increased vascularization of the mantle (DESHPANDE, 1957; FRETTER & GRAHAM, 1962) may enhance aerial oxygen uptake in some high shore trochids (NEWELL, 1973) but it is not clear whether *Notoacmea* possesses any structural adaptations to promote aerial gas exchange.

The ratio of aquatic to aerial oxygen consumption of *Notoacmea pileopsis* is very similar to that of the patellid limpet *Cellana radians* (Table 1) whose oxygen uptake did not change significantly between aquatic and aerial environments at 10°C (Figure 2). Patellid limpets, whose principal respiratory organs are secondary pallial gills (PURCHON, 1968), generally appear well adapted for aerial oxygen uptake (Table 1), although aquatic to aerial ratios vary with size and temperature and may be modified to meet the overall energy balance of individual species (BRANCH & NEWELL, 1978; BRANCH, 1979; NEWELL & BRANCH, 1980).

The patterns of aerial oxygen consumption displayed by *Notoacmea pileopsis* and *Cellana radians* immediately after emersion and after periods of desiccation are remarkably similar (Figure 3). The oxygen uptake of both species decreased significantly after a relatively short (1

h) period of desiccation, and remained relatively constant during subsequent drying. It therefore appears that prosobranch limpets have two levels of aerial oxygen consumption: (1) a rate immediately on emersion (in this instance similar to the aquatic rate) and (2) a depressed rate indicative of desiccation stress (COLEMAN, 1976).

The decrease in aerial oxygen consumption of *Notoacmea pileopsis* after a period of desiccation is very similar to that reported for other acmaeids (BALDWIN, 1968), and the vertical range of this limpet does not appear to be correlated with any adaptations to minimize the respiratory effects of drying (Table 2). With the reservations that Table 2 contains limited data and comparisons are made using gastropods of different size ranges (WOLCOTT, 1973) there is some indication of a correlation between the principal organ of gas exchange and the effect of desiccation on aerial oxygen uptake. Desiccation appears to have a greater effect on the oxygen uptake of acmaeid limpets (BALDWIN, 1968; present study) than that of limpets possessing pallial gills (present study) or other prosobranchs with modified respiratory organs (SANDISON, 1966; SHIRLEY *et al.*, 1978).

The greater decrease in oxygen uptake during desiccation reported for acmaeids (Figure 3; Table 2) may involve the production of mucus slowing down both water loss (WOLCOTT, 1973) and oxygen uptake. In addition, the gill filaments may clump together during drying to occlude a large area of the respiratory surface.

The depressed rates of aerial oxygen uptake reported for *Notoacmea pileopsis* and *Cellana radians* during desiccation may conserve energy during aerial exposure (BRANCH & NEWELL, 1978; BRANCH, 1979; NEWELL & BRANCH, 1980). The desiccated rates in both instances are, however, significantly lower than the resting aquatic rate, and, if aerobic metabolism in air were to fall below the minimum maintenance level (NEWELL, 1979), then anaerobic metabolism may become important (BAYNE *et al.*, 1976; WIESER, 1980).

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Predator Deterrence by Flexible Shell Extensions of the Horse Mussel *Modiolus modiolus*

by

MARY M. WRIGHT AND LISBETH FRANCIS

Biology Department, Bates College,
Lewiston, Maine 04240

Abstract. Flexible, tapering hairs, or awns, on the periostracum of the horse mussel *Modiolus modiolus* discourage attachment by the predatory whelk *Thais lapillus*. This conclusion is based on laboratory preference tests demonstrating a higher frequency of attachment to the hairless blue mussel *Mytilus edulis*. Removal of the awns of the horse mussel results in more nearly equal attachment to both mussel species. To our knowledge, this is the first time that a selective advantage has been demonstrated experimentally for any periostracum.

INTRODUCTION

TWO MUSSEL species occur commonly along the rocky coast of Maine. The blue mussel *Mytilus edulis* (Linnaeus, 1758) is found in bays and estuaries and on exposed promontories at various levels in the mid to low intertidal (SEED & BROWN, 1975; MENGE, 1976). In contrast, the horse mussel *Modiolus modiolus* (Linnaeus, 1758) extends from the low intertidal to subtidal regions (BROWN & SEED, 1977).

The most obvious morphological difference between the shells of these two mussels is the awns (hairy projections of the periostracum at the exposed posterior margin), which are present on *Modiolus modiolus* but are absent from *Mytilus edulis*.

The dog whelk *Thais lapillus* (Linnaeus, 1758) is a major intertidal predator that commonly attacks the blue mussel (MENGE, 1976), and at least occasionally attacks the horse mussel (personal observation, MMW). *Thais* attacks bivalves mechanically by drilling with the radula, and chemically by dissolving the shell with secretions from the accessory boring organ (GABRIEL, 1981).

SEED & BROWN (1975) report that during their laboratory experiments, *Thais lapillus* never attacked the horse mussel; NIELSEN (1975) suggests that the hairy or spiny shell texture may discourage attack by *Buccinum undatum* Linnaeus, 1758, a whelk that attacks bivalves by wedging the lip of its own shell between the open valves to hold them apart, then reaching in to tear off bits of flesh.

We suspect that the hairy periostracum of *Modiolus modiolus* might discourage attachment and boring by *Thais*

lapillus, which depends on prolonged, close contact with prospective prey in order to attack and consume it.

Previous to this study, the only characteristic of bivalve shells actually shown to hamper predation by drilling gastropods was a greatly thickened valve (Vermeij, 1978).

MATERIALS AND METHODS

Collection and Holding of Animals

Animals were collected occasionally from 16 October 1982 to 9 March 1983 on Bailey Island, Maine, a few hundred meters from a section of rocky exposed coastline called "The Giant Staircase." Freshly caught whelks were isolated from prey and allowed to adapt to aquarium conditions for at least 4 days.

All animals were kept in a filtered recirculating seawater system in which one third of the water was replaced each week by ocean water that had been collected and allowed to stand for at least a week. Temperature, salinity, and pH were maintained within natural limits (8.5 to 11°C; 28 to 32 ppt.; and 7.4 to 7.5 respectively). The tanks received light from several large windows nearby and from fluorescent ceiling lights.

Design of Predator Choice Experiments

Three mussels of each species were selected, approximately matched for size (4 to 8 cm long), and arranged alternately on a sheet of plastic at one end of a five gallon aquarium. In each trial a different set of 20 whelks was placed in rows with their anterior ends directed toward

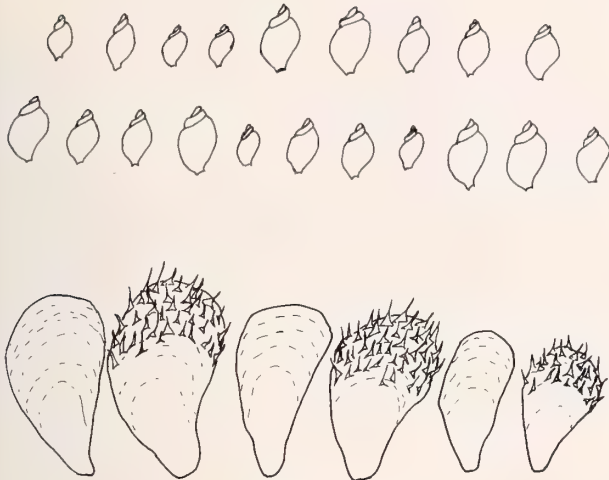


Figure 1

Spacing and arrangement of mussels (*Modiolus modiolus* with the awned periostracum, and *Mytilus edulis* with the smooth periostracum) and whelks (*Thais lapillus*) at the outset of laboratory predator choice trials.

the posterior margins of the mussels (Figure 1). This seemed a suitable testing arrangement, because in the field the mussels usually are wedged into crevices or between neighboring mussels with only the posterior margins exposed. After 24 h the number of whelks actually attached to each species of mussel was recorded. To minimize the possibility that the whelks were following old whelk mucus trails from previous trials, a new sheet of plastic was secured to the bottom of the tank and the mussels were scrubbed with a wet brush before each trial.

In a second set of experiments, the shells of all mussels were scraped with a razor blade before they were placed in tanks. This treatment effectively removed the awns of *Modiolus modiolus*.

RESULTS

With the periostracum of the mussels intact, 142 of the whelks attached to the smoother valves of *Mytilus edulis*, while only 23 attached to the hairy valves of *Modiolus modiolus* (31 trials involving 620 whelks). In these trials, the whelks attached to *Mytilus edulis* much more frequently than predicted by chance (Chi-square test for goodness of fit, $\chi^2 = 86$, $P \ll 0.001$). When all of the mussels were scraped, which effectively removed the awns from the horse mussel, a total of 99 whelks attached to *Mytilus edulis*, while 72 attached to the awnless specimens of *Modiolus modiolus* (28 trials involving 560 whelks). While the whelks continued to show a slight preference for *Mytilus edulis* when the awns of *Modiolus modiolus* were removed ($\chi^2 = 8.5$, $P < 0.005$), this preference was much less marked than when the periostracum was intact (2×2 test of independence, $\chi^2 = 73$, $P \ll 0.001$).

DISCUSSION

Along the rocky intertidal of New England, natural or artificial exclusion of the predatory whelk *Thais lapillus* results in monopolization of the primary space by *Mytilus edulis*, while in areas of heavy whelk predation, the blue mussel is commonly eliminated (MENGE & SUTHERLAND, 1976). Intense predation by invertebrates of the lower shore and subtidal apparently prevents the establishment of subtidal populations of *Mytilus edulis* (SEED, 1969).

Predation levels are higher and survival rates lower for small specimens of *Modiolus modiolus* than for larger ones, and rapid growth of smaller individuals results in escape in size from predation (SEED & BROWN, 1975). This kind of selective pressure should favor the evolution of mechanisms that discourage predation, especially on smaller individuals.

Our experiments show that the shell awns of *Modiolus modiolus* are an effective predator deterrent discouraging attachment by the whelk *Thais lapillus*. The fact that smaller horse mussels have more awns may be another indication of the importance of predation and predator deterrence among small, vulnerable individuals. The presence of these protective shell awns may allow *Modiolus modiolus* to live below *Mytilus edulis* in the lower intertidal and subtidal, where predator pressure is relatively intense. Further work is presently under way to determine whether the awns also discourage attack by other common predators such as the starfish *Asterias vulgaris* (MENGE, 1979).

It is possible that shell awns and various other kinds of shell sculpturing are advantageous not only because they make attachment more difficult, but also because they make an undesirable prey species easy for a prospective predator to recognize and reject. Using crabs as predators and mussels as prey, ELNER & HUGHES (1978) demonstrated the importance of recognition time in determining the selectivity of a predator. Foraging theory predicts that a predator that cannot distinguish quickly between a preferred prey item and a common, less desirable one, will take relatively large numbers of the less preferred type. Anything that makes a less preferred prey species easy to recognize could have a large selective advantage in such a situation. In addition to making *Modiolus modiolus* more difficult to approach and attack, the awns on the shell may make this species easier to recognize and reject by predators searching for more desirable prey.

While there has been considerable work on the structure and formation of the periostracum (reviewed by SALEUDDIN & PETIT, 1983; WAITE, 1983), there has been little experimental work on periostracum function (reviewed by CLARK, 1976). In general, the periostracum is presumed to protect the calcareous layers of the shell from erosion (FRETTER & GRAHAM, 1962; SOLEM, 1974) and to play an important role in mineralization of the shell (CLARK, 1976).

This is the first demonstration that the periostracum of a bivalve can discourage predation by a drilling gastropod.

To our knowledge, it is also the first time that a specific selective advantage has been demonstrated experimentally for any periostracum.

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The Opisthobranchs of Cape Arago, Oregon, with Notes on Their Biology and a Summary of Benthic Opisthobranchs Known from Oregon

by

JEFFREY H. R. GODDARD

Oregon Institute of Marine Biology,
Charleston, Oregon 97420

Abstract. The opisthobranch mollusks from Oregon have not been well studied, and little or nothing is known about the biology of many species. The present study consisted of field and laboratory observations on the biology and ecology of Cape Arago opisthobranchs. Forty-six species were found, extending the range of six northward and two southward. New food records are presented for ten species; 21 species were observed feeding on previously recorded prey. The egg masses of a number of species are described for the first time, and developmental data are given for 21 species. Twenty produce planktotrophic larvae, and *Doto amyra* produces lecithotrophic larvae, the first such example known from eastern Pacific opisthobranchs. *Hallaxa chani*, whose diet consists solely of the sponge *Halisarca* sp., appears to be the first eudoridacean nudibranch known to have a subannual life cycle. Its rapid life cycle appears to be adaptive primarily in exploiting the widely dispersed and fast growing *Halisarca* sp. Data presented on the longevity of *Cadlina luteomarginata* and *C. modesta* suggest they have annual life cycles. Nudibranchs appear to be among the most important predators of intertidal encrusting animals at Cape Arago and probably significantly affect the diversity of the encrusting community. Sixty-six species of benthic opisthobranchs are currently known from Oregon.

INTRODUCTION

THE OPISTHOBRANCH mollusks of Oregon have been little studied compared with those of California to the south and those of the San Juan Archipelago-Vancouver Island region to the north. SOWELL (1949) studied the natural history of opisthobranchs in the Coos Bay-Cape Arago area in the late 1940's and listed 19 species from that area. Since then two relatively brief studies of Oregon opisthobranchs have been made. SPHON (1972) reviewed the literature mentioning Oregon opisthobranchs and reported on a six-day collecting trip made in five Oregon localities. BELCIK (1975) lists species not reported by Sphon that he found in the Coos Bay-Cape Arago area while studying parasites of mollusks and fish. A total of 43 benthic opisthobranchs were reported in these three studies, 21 from Cape Arago.

Members of the order Nudibranchia comprise most of the rocky intertidal opisthobranchs. Although little is known about the biology and ecology of many northeast-

ern Pacific species (BEEMAN & WILLIAMS, 1980), those nudibranchs that have received study have all been shown to be carnivores that prey, as a group, on a wide variety of sessile invertebrates (THOMPSON, 1976; McDONALD & NYBAKKEN, 1978; BEEMAN & WILLIAMS, 1980). Little is known about the effects of their predation on the encrusting animal communities to which they belong.

In this paper I report on observations, scattered over a 45-month period beginning in December 1979 and ending in September 1983, of rocky intertidal opisthobranchs from Cape Arago. The purpose of this research was to (1) determine which species occur at Cape Arago, (2) examine aspects of their biology, including food, feeding methods, larval development, and, in a few cases, life cycles, and (3) attempt to gain some understanding of the effects of nudibranch predation on the encrusting animal community at Cape Arago. Observations are presented for each of the 46 species I found, followed by a general discussion and comments on the benthic opisthobranchs currently known from Oregon.

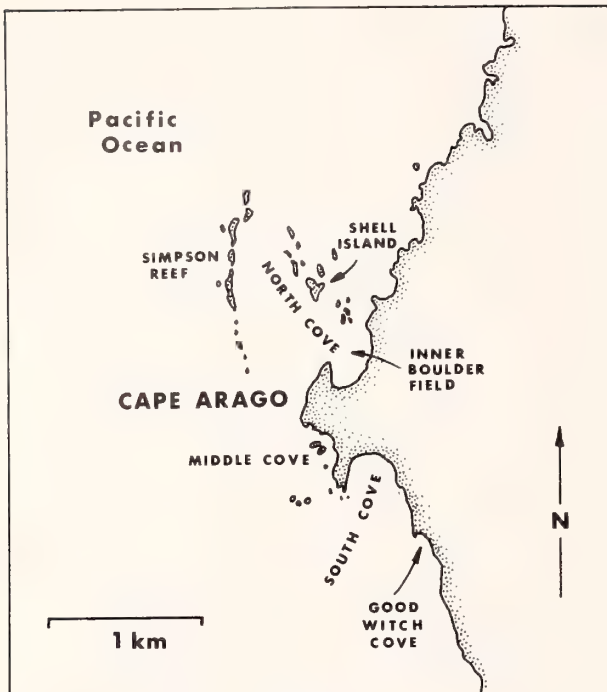


Figure 1

Cape Arago, Oregon (43°20'N, 124°22'W).

STUDY AREA AND DATES OF FIELD OBSERVATIONS

Cape Arago contains one of the widest, most physically and biologically diverse intertidal areas between Cape Mendocino, California, and Cape Flattery, Washington (P. W. Frank and J. J. Gonor, personal communications; personal observations). The study area included North, Middle, and South coves of Cape Arago and one small cove located just south of Cape Arago which I call Good Witch Cove (Figure 1). Cape Arago is situated 7.3 km southwest of the entrance to Coos Bay. Charleston and the Oregon Institute of Marine Biology (O.I.M.B.) are located just inside the south side of the mouth of Coos Bay.

North Cove

North Cove has the largest intertidal area of the four coves. At low tide one can walk beyond Shell Island to the outer boulder field and edge of the *Macrocystis-Nereocystis* kelp bed located just inside Simpson Reef. North Cove contains a mixture of sandstone shelves, outcrops, and boulders of variable size and is protected from large surf by Simpson Reef. Forty-two of 65 trips comprising this study were made to the inner boulder field, one of the most sheltered parts of North Cove (Figure 1). This boulder field consists of roughly half fissured-and-pocketed bedrock and half boulders averaging 0.25 to 0.5 m in

diameter. During the calmer months (spring and summer) much of the inner boulder field is subject to silt and detritus accumulation. Few sea urchins are present, and the area is dominated by the algae *Egregia menziesii*, *Hedophyllum sessile*, *Iridea flaccida*, *Cystoseira osmundacea*, *Laminaria* sp., the introduced *Sargassum muticum*, and the surfgrass *Phyllospadix*. The undersides of boulders and ledges support a rich variety of sessile invertebrates—the prey of most nudibranchs—and it is under and among these boulders that the greatest number of opisthobranch species and individuals occurring at Cape Arago are found (38 out of the Cape Arago total of 46).

A total of 44 trips was made to North Cove in the following months: 12/'79; 3, 5, 6, 7/'80; 6/'81–5/'82; 8, 9/'82; and 3–9/'83. Trips from 10/'81 to 2/'82 were at night and covered a relatively small portion of the inner boulder field.

Middle Cove

Middle Cove contains the next largest intertidal area of Cape Arago, and, like North Cove, contains a mixture of sandstone bedrock, boulders, and outcrops of varying size. However, Middle Cove is more exposed to surf and possesses a number of invertebrates rare or absent in the North Cove inner boulder field. Among these are the hydrocoral *Allopora porphyra* (Fisher, 1931), the coral-like ectoproct *Heteropora alaskensis* Borg, 1933, and the solitary coral *Balanophyllia elegans* Verrill, 1864. An undescribed white alcyonacean octocoral (see *Tritonia festiva*) is abundant. Where sea urchins are sparse, Middle Cove supports diverse and luxuriant invertebrate and algal communities. Middle Cove appears to possess the highest hydroid and sponge diversity of any of the coves. In ten trips here (made in the months of 3, 7, 8/'80; 6, 8/'81; 5–8/'83) I found 28 species of opisthobranchs.

South Cove

The west side of South Cove consists of a small boulder field semi-protected from surf. As one moves toward the point separating Middle and South coves, surf exposure increases and the substrate becomes solid rock with deep surge channels. Not as many species and individuals of opisthobranchs occur at South Cove. I found 10 species on five trips (2, 5/'80; 5/'81; 6, 7/'82), and none of the species was ever abundant. The low number of opisthobranchs here may be related to the smaller size of the low-intertidal boulder field—much of the area consists of urchin or *Phyllospadix*-dominated bedrock. For unknown reasons, hydroids are rare at South Cove.

Good Witch Cove

This is the most surf-exposed of the coves and is accessible only on the lowest tides when the swell is small. The substrate consists of pocketed-and-fissured bedrock overlain with patches of boulders. Many of these boulders are

relatively barren of organisms—probably the result of grazing by the large numbers of urchins, limpets, and chitons present and perhaps also the result of boulder-overturning by surf. However, the undersides of many ledges and larger boulders support a rich invertebrate fauna. I found 18 opisthobranch species here on six trips (5, 6, 7/'80; 5/'82; 5, 7/'83).

METHODS

Opisthobranch prey species were determined by observing close association of the opisthobranch and its possible prey in the field and by laboratory observation of feeding. Gut contents also were occasionally examined.

Observations on egg masses and larval development were largely restricted to species for which no other data currently exist. To make these observations, opisthobranchs were first separated by species into dishes or jars. A newly laid egg mass was scraped off the side of the container, examined, and transferred to a separate, labelled jar. The water in these jars was changed every one or two days, and all jars were kept in a flowing seawater bath (10 to 17°C). Separated egg masses were examined daily until veligers had hatched, at which time veliger shell lengths were measured. All measurements of eggs and veligers were made with a compound microscope equipped with an ocular micrometer.

Due to the discontinuity of field observations little can be concluded about the seasonality of most of the opisthobranch species. North Cove was observed in every month of the year (though continuously only for one year), and conclusions about seasonality are presented for a few of the species found there. These should be considered tentative.

NATURAL HISTORY OBSERVATIONS

Acanthodoris nanaimoensis O'Donoghue, 1921

This dorid occurred rarely at all four coves. I found a total of seven specimens ranging in length from 5 to 22 mm in February, May, July, and December.

Adalaria sp.

I found ten specimens of this white dorid, ranging in length from 4 to 15 mm in March, April, August, and September at North Cove. Sandra Millen (personal communication) informs me that this is one of three *Adalaria* species found in British Columbia and is not species 138 in BEHRENS (1980). She further states: "It can be recognized by the elongate body, wider at the front end, and by the spicules which project out of the top of the tubercles in a radiating pattern."

Five *Adalaria* sp. were found on the anascan bryozoan *Hincksina minuscula* (Hincks, 1882) on the undersides of boulders. Laboratory observations confirmed that *Adalaria* sp. feeds on this bryozoan. Members of the Onchidoridi-

dae are known to use the radula to open the frontal membranes or opercula of their bryozoan prey and then to use a muscular buccal diverticulum as a pump to suck out the zooids (THOMPSON, 1976). After placing fresh pieces of *Hincksina minuscula* with *Adalaria* sp. specimens for a day, such feeding was evidenced by the many empty zooecia possessing partially attached frontal membranes.

The egg mass of *Adalaria* sp. is a white ribbon laid on edge in a coil of 2 to 4 turns. Egg masses are 1–2 mm high and 4–10 mm in diameter. For data on the larval development of this and other species see Table 1.

Aeolidia papillosa (Linnaeus, 1761)

This eolid is frequent at North Cove. Specimens ranged in length from 5 to 55 mm and often occurred next to *Epiactis prolifera* Verrill, 1869, an abundant anemone upon which *Aeolidia papillosa* readily feeds in the laboratory (personal observation).

Aldisa cooperi Robilliard & Baba, 1972

I found three specimens, one at Middle Cove in June 1981, and two at Good Witch Cove in May and July 1983. The first two were 22 mm and 27 mm long respectively and orange-yellow in color; they had, respectively, 9 and 8 small black spots on the midline of the dorsum between the rhinophores and gills. The third specimen was yellow and also possessed a number of small black spots on the midline.

Aldisa cooperi was originally described as a subspecies of *Aldisa sanguinea*. However, BERTSCH & JOHNSON (1982), on the basis of sympatry, and Millen (personal communication), on the basis of anatomy, consider them to be separate species. With this in mind, I kept one specimen of both species together in a jar to see if mating and egg-laying would occur. The specimen of *A. cooperi* measured 27 mm in length, and that of *A. sanguinea* 20 mm. After one month in captivity (12–16°C), and what appeared to be a number of matings, the specimen of *A. sanguinea* laid an egg mass. The embryos stopped developing at about the 32-cell stage. Although I cannot rule out other factors, this may indicate that interbreeding occurred but resulted in inviable hybrid embryos, thus supporting the conclusion that *A. cooperi* and *A. sanguinea* are distinct species.

Aldisa sanguinea (Cooper, 1863)

One bright-red specimen, 26 mm long and lacking dark spots on the dorsum, was collected at North Cove by the spring 1982 Oregon Institute of Marine Biology invertebrate zoology class. I found another specimen, red-orange in color, 20 mm long, and also lacking dark spots, at Good Witch Cove in May 1983. Specimens of *Aldisa sanguinea* reported from Cape Arago by SOWELL (1949) were red-orange and also lacked dark spots.

Though of weak taxonomic utility, color pattern is the

only character I have used to distinguish *Aldisa sanguinea* from *Aldisa cooperi*. *Aldisa cooperi* is yellow to orange and apparently always has small black spots on the midline of the dorsum (ROBILLIARD & BABA, 1972; BEHRENS, 1980); *A. sanguinea* is red, occasionally yellow-orange to yellow-green, with zero to two relatively large dark spots on the dorsal midline (MCDONALD & NYBAKKEN, 1980). If specimens of *A. cooperi* are found that lack any dark spots, then the identification of the above Cape Arago specimens as *A. sanguinea* will become questionable. More work is clearly needed on these two species. Unfortunately, all I possess of the two specimens of *A. sanguinea* I saw is the radula from the 26 mm specimen.

Ancula pacifica MacFarland, 1905

This species is frequent at North Cove and was most common during spring and early summer. *Ancula pacifica* usually occurred under boulders, and in June 1983 I found eight specimens with egg masses among the entoproct *Barentsia* sp. on the undersides of boulders. Many of these *Barentsia* lacked a calyx—most likely as a result of grazing by *Ancula pacifica*. *Ancula pacifica* is known to feed on *Barentsia ramosa* (Robertson, 1900) in California (MCDONALD & NYBAKKEN, 1978).

Before spring 1983, all the *Ancula pacifica* I had observed at Cape Arago had the color pattern described by ROBILLIARD (1971b) for the two specimens he found in Washington. These specimens lack orange lines on the body but do possess orange-tipped rhinophores, accessory rhinophore papillae, gills, and extrabranchial papillae. In spring and summer 1983 I noticed the above form of *Ancula pacifica* as well as the more typical form (which has orange lines on the body and is common in California) at North Cove. Northern and southern forms of *Ancula pacifica* may exist.

The egg mass of *Ancula pacifica* is a white, slightly flattened, tapering cord. The cord is not laid in a spiral.

Anisodoris lentiginosa Millen, 1982

On 18 May 1980 I found one specimen crawling on bare rock in a pool at Good Witch Cove. It was about 90 mm long, pale yellow in color, and had six small, dark brown blotches scattered on the central part of the anterior two-thirds of the dorsum (Figure 2). This specimen represents a southern range extension of 615 km and is the first intertidal record of the species (MILLEN, 1982).

Anisodoris nobilis (MacFarland, 1905)

Anisodoris nobilis is moderately common at Cape Arago, occurs at all four coves, and can be found all year long at North Cove. I observed specimens less than 10 mm long in December and April. One March specimen measured about 200 mm in length. In the field *A. nobilis* was found feeding on the yellow sponges *Mycale macginitiei* de Lau-

benfels, 1930, *Zygherpe hyaloderma* de Laubenfels, 1932, *Tedania gurjanovae* Koltun, 1958, and *Lissodendoryx firma* (Lambe, 1895). *Anisodoris nobilis* readily feeds on these sponges in the laboratory, and three individuals also ate *Ophlitaspongia pennata* (Lambe, 1895) in the laboratory. *Tedania gurjanovae* and *Ophlitaspongia pennata* are new food records for *A. nobilis* (MCDONALD & NYBAKKEN, 1978; BLOOM, 1981).

On 30 April 1982 I found one *Anisodoris nobilis* about 50 mm long under a boulder feeding on an individual of *Lissodendoryx firma* covering an area of 680 cm² (total boulder undersurface = 4900 cm²). Some of the sponge had already been grazed off the rock. On 21 August 1982 only a few square centimeters of the sponge remained and no individuals of *A. nobilis* (nor any other possible predators of the sponge) were present. Though I cannot rule out that other *A. nobilis* or other predators of *L. firma* had visited the rock, it is possible that the above specimen of *A. nobilis* ate all of the missing sponge.

By area covered, *Zygherpe hyaloderma* is the most abundant of the yellow sponges at North Cove (personal observation). *Mycale macginitiei*, which covers considerably less area (but is a thicker sponge) is next most common. Preliminary observations suggest that *Anisodoris nobilis* prefers *Mycale macginitiei* over *Zygherpe hyaloderma* but will sometimes eat the first of these sponges it contacts, even when the two are in close proximity. Further study of the food preferences of *Anisodoris nobilis* and the effects of length of starvation, previous diet, and age would be interesting.

The ribbon of one egg mass laid by a 140-mm long individual measured 2.7 × 40 cm and contained about 2.1 million eggs.

Aplysiopsis smithi (Marcus, 1961)

This sacoglossan occurred in a few high-intertidal pools between South and Good Witch coves. I examined these pools for *Aplysiopsis smithi* monthly from June 1980 through July 1981. The sacoglossan and its egg masses were abundant in late spring and early summer 1980, and, with the exception of one specimen found in December 1980, disappeared in September 1980 and did not reappear until May 1981. It was abundant until at least July 1981, though not as common as in the previous year. In these pools *A. smithi* feeds exclusively on the green alga *Cladophora* sp. GREENE (1970) reported southern California *A. smithi* feeding on *Cladophora trichotoma*.

My observations of the egg masses and veligers match those of GREENE (1968). He observed white and yellow colored egg masses. I noticed that laboratory specimens laid yellow egg masses at first, but later egg masses were faint yellow to white. The newly hatched planktotrophic veligers lack eyespots and possess a granular black pigment scattered on the edge of the mantle that folds over the outer lip of the shell. Such pigmentation is unique among the veligers observed in this study.

Archidoris montereyensis (Cooper, 1863)

Archidoris montereyensis is fairly common at Cape Arago and occurs year-round. Specimens ranged in length from 4 to 65 mm. Individuals less than 10 mm long were found from November to April, and individuals greater than 50 mm were observed in December, January, April, May, and July. Eggs were observed in the field in May and July. I sometimes found *A. montereyensis* stranded out of water next to or on *Halichondria panicea* (Pallas, 1766) and on the massive and densely spiculate sponge *Suberites* sp. One specimen, 10 mm long, was found at Good Witch Cove embedded in a soft, unidentified, orange, encrusting sponge.

Archidoris odhneri (MacFarland, 1966)

This species is quite common at Good Witch and Middle coves but also occasionally occurs at North and South coves. With the exception of one 13 mm long specimen found in June 1983 at North Cove, all specimens were 70–100 mm long. *Archidoris odhneri* rarely occurred on sponges. Two specimens, including the above 13 mm individual, were on *Hymeniacidon ungodon* de Laubenfels, 1932, and ate this sponge in the laboratory. One 90-mm long specimen, brownish-yellow in color (and the only specimen of *A. odhneri* I found that was not pure white), was found on a large *Suberites* sp. individual of the same color; the sponge appeared to have been grazed. *Archidoris odhneri* has not been reported feeding on either of these sponges (McDONALD & NYBAKKEN, 1978; BLOOM, 1981).

Berthella californica (Dall, 1900)

This pleurobranchomorph is common on the submerged, relatively barren boulders at Good Witch Cove and also occurs occasionally at the other three coves. BEHRENS (1980) considers *Pleurobranchus denticulatus* MacFarland, 1966 to be synonymous with *Berthella californica* and gives Crescent City, California as the northern range limit of *B. californica*. However, LAMBERT (1976) reported *Pleurobranchus denticulatus* from Pearse Island, British Columbia.

The egg mass of *Berthella californica* is a white ribbon, 3–4 mm wide, laid on edge in a loose spiral. The newly hatched veligers are distinctive in possessing a dark, red wine colored patch of tissue on the right side next to the anus, as well as a shell whose oldest portion has a brown tinge (similar to the pigmentation on the veliger shells of *Hallaxa chani*, but not as dark or extensive).

Cadlina luteomarginata MacFarland, 1966

This species is moderately common at all the coves of Cape Arago. I occasionally found it feeding on the pink sponge *Aplysilla glacialis* (Dybowski, 1880). This sponge has previously been reported as the food of *Cadlina flavo-*

maculata MacFarland, 1905, and *C. modesta*, but not *C. luteomarginata* (McDONALD & NYBAKKEN, 1978). One individual was found feeding on a light grayish-tan colored *A. glacialis* individual, and a number of *C. luteomarginata* starved in the laboratory fed on *Halisarca* sp. One specimen, 23 mm long at collection, has survived seven months in the laboratory without any food except for one day of feeding on *Aplysilla glacialis* one month after collection.

On 1 May 1982 I noted a specimen of *Aplysilla glacialis* covering an area of 126 cm² on the underside of a North Cove boulder. The boulder had 630 cm² of undersurface. I tagged the boulder to keep track of the sponge. On 21 August 1982 one 27 mm specimen of *Cadlina luteomarginata* and a 15 mm *Cadlina modesta* were observed feeding on this *Aplysilla*. They had eaten 18 cm² of the sponge, but the sponge had grown an approximately equal amount since May. On 26 March 1983 both slugs were still present (though I cannot rule out that they were different individuals or that additional individuals of *Cadlina* had visited the rock) and had eaten all but 4.5 cm² of the sponge. The *C. luteomarginata* measured 42 mm and had laid two egg masses (one recently laid; the larvae of the other had already hatched). The *C. modesta* measured 20 mm. On 15 April 1983 both dorids were gone and only a trace of *Aplysilla* remained.

O'DONOGHUE & O'DONOGHUE (1922:138) stated that the egg masses of *Cadlina luteomarginata* "were not found so frequently as those of *Archidoris montereyensis* and *Diaulula sandiegensis* although the animal itself is quite common," and COSTELLO (1938:331) noted that "the egg ribbons are less vertical than in . . . other forms." My observations agree with both statements. I saw only two egg masses in the field, both in March 1983. The white egg mass ribbon slants toward the center of the tightly wound coil and overlaps itself in the preceding turn. One egg mass had five turns and a diameter of 16 mm. DEHNEL & KONG (1979) described aspects of the egg mass of *Cadlina luteomarginata* but did not mention the angle of the ribbon or tightness of the coil. Egg masses of *C. luteomarginata* may be more common subtidally than intertidally.

Cadlina modesta MacFarland, 1966

Before April 1982 I had only seen two specimens of *Cadlina modesta* at Cape Arago. After April 1982 I found 15 specimens. All 17 specimens were observed in spring and summer at North Cove. Two individuals were feeding on *Aplysilla glacialis* and two on *Halisarca* sp., a previously unreported sponge prey. One individual, 6 mm long and found on *Halisarca* sp., survived in the laboratory at 8–16°C for 17.2 months. This specimen was sporadically fed *Halisarca* sp. for the first 5 months, and grew to 20 mm in length. It was then starved for 6 months. During the following 6 months it was again sporadically given *Halisarca* sp., and it ate a total of 13 cm² of the sponge (*Halisarca* sp. averages 2 to 3 mm in thickness). The specimen

did not appear to eat any of the *Halisarca* sp. present for the last month of its life, and it never laid eggs.

Concerning the color of the rhinophores of *Cadlina modesta*, MACFARLAND (1966) wrote "rhinophores light, seldom dusky," and BERTSCH (1969) stated "the color of the rhinophores varied from whitish to dusky brown." In laboratory specimens of *Cadlina modesta* the rhinophores changed from whitish or light yellow to brown with increasing age.

The egg mass of *Cadlina modesta* is a cream colored ribbon 2–3 mm high laid in a loose spiral of 1 to 3 turns. Mean egg mass area was 115.3 mm² (SD = 52.0, n = 13 egg masses laid in laboratory by three specimens 15–20 mm long). At a mean density of 180 eggs per mm² of egg mass (SD = 33, n = 3), the "average" egg mass of *Cadlina modesta* contains about 20,750 eggs.

Catriona columbiana (O'Donoghue, 1922)

Catriona columbiana is frequent at Cape Arago and was usually on, or near, the stolons of *Tubularia marina* (Torrey, 1902) on which it feeds. *Catriona columbiana* appears to be most abundant in spring and summer, particularly at North and Middle coves. Two color forms exist, one with orange cephalic tentacles and one with white cephalic tentacles (both forms have orange on the distal half of the rhinophores). I did not observe any differences in the radula, mandibles, egg masses, or veligers of these two forms.

This species lays small, sac- to crescent-shaped egg masses (type D of HURST, 1967). There is one egg per capsule, and the capsules are deposited in an irregular coil, 2–3 capsules wide, in the egg mass.

Crimora coneja Marcus, 1961

With the exception of a single specimen reported from "near Humboldt Bay, Humboldt County, California" (McDONALD, 1983), this delicate and rare dorid was previously known only from the type locality of Point Loma, San Diego County, California (BEHRENS, 1980; McDONALD, 1983). On August 29, 1981 Katheryn Young and Tom Wayne of O.I.M.B. collected two individuals from under a boulder in the North Cove inner boulder field (Figure 3). Both specimens were 16 mm long. Since then I have observed seven specimens, ranging in length from 14 to 19 mm, at North Cove (one in December 1981, one in April 1983, two in August 1983, and three in September 1983) and one 12 mm specimen at Middle Cove in July 1983. These eight specimens were on *Hincksina minuscula* on the undersides of boulders approximately 0.3 m in diameter.

Laboratory observations confirmed that *Crimora coneja* feeds on *Hincksina minuscula*. One individual overnight ate almost every zooid in a 1 cm² piece of the bryozoan. The zooecia were empty and the frontal membranes missing, indicating that *Crimora* uses its radula to rasp out entire zooids (in contrast to the feeding method of *Adalaria* sp.).

The egg mass of *Crimora coneja* is a thin ribbon laid flat (not on edge as in most dorids) in a spiral of 4 to 6 turns, and measures 9–12 mm in diameter. The ribbon is about 1 mm wide, contains 1–2 layers of eggs and lacks striations of any sort. In different egg masses the eggs vary from white to pale orange in color. Because of its thinness and form, the egg mass is difficult to discern when laid on bryozoan-encrusted substrates.

Cuthona abronia (MacFarland, 1966)

This eolid can be common during the spring and summer at North and Middle coves. Although occasionally seen crawling on submerged algae or on the surface of calm tidepools, it usually occurs among minute, unidentified, thecate hydroids under boulders in areas subject to little accumulation of silt and detritus (purple sea urchins are often in the vicinity). In April 1982 I found five specimens and about 20 egg masses on the underside of a single small boulder.

Cuthona albocrusta (MacFarland, 1966)

Cuthona albocrusta occurred at Middle Cove (two specimens in August 1980 and four in July 1983) and North Cove (five in May 1980, one in July 1981, and over 11 in July and August 1983). In August 1983 I found five specimens clustered among minute, unidentified, unbranched, thecate hydroids (probably of the family Campanulinidae). These hydroids were partially covered by a fine, light grayish-tan colored silt. The eolids were quite cryptic in this microhabitat.

Cuthona cocoachroma Williams & Gosliner, 1979

Three specimens of this rare eolid were seen at Middle Cove, one in July 1980, one in June 1981, and one in June 1983. The range of *Cuthona cocoachroma* is extended 255 km from Trinidad Head, Humboldt County, California (JAECKLE, 1981). I also found one specimen of *C. cocoachroma* at Cape Blanco (50 km south of Cape Arago) in April 1982.

The egg mass of *Cuthona cocoachroma* is a white cord laid in a small rosette.

Cuthona flavovulta (MacFarland, 1966)

I found seven specimens crawling on submerged algae or on the surface of calm pools at Middle and North coves in summer 1983. The range of *Cuthona flavovulta* is thus extended from Palmer's Point, Humboldt County, California (JAECKLE, 1981).

Cuthona fulgens (MacFarland, 1966)

Four specimens were found crawling on submerged algae or on the surface of calm pools at North and Middle coves in summer 1983. The range of *Cuthona fulgens* is

extended from Duxbury Reef, California (GOSLINER & WILLIAMS, 1970).

Dendronotus frondosus (Ascanius, 1774)

I observed few *Dendronotus frondosus* at Cape Arago until June and July 1983, when over 20 specimens were seen on a small unidentified species of *Obelia* in the very low intertidal of Middle Cove. *Dendronotus frondosus* can be abundant during the spring and summer, feeding on the much larger and highly branched species of *Obelia* on the docks of the Charleston boat basin (personal observations). All Cape Arago specimens were less than 20 mm long, and a number of individuals were on hydroids growing on the brown alga *Cystoseira*. *Dendronotus frondosus* occurred in low numbers at all the coves of Cape Arago.

Dendronotus subramosus MacFarland, 1966

I found only two specimens of *Dendronotus subramosus* at Cape Arago, both at Middle Cove. One specimen, 4 mm long, was under a small boulder, and one 2 mm specimen was on hydroid-covered *Cystoseira*.

Diaphana californica Dall, 1919

One specimen, with a 3-mm long shell, of this minute bullomorph was collected from the North Cove inner boulder field in August 1981. I found three more (shell lengths of 3.3 mm, 3.0 mm, and 2.1 mm) in the same location in September 1983. Much of the mantle and viscera is visible through the thin translucent shell. The range of this species is extended 610 km from Duxbury Reef, California (GOSLINER & WILLIAMS, 1970).

The egg mass of *Diaphana californica* is a fragile and very extensible cord attached to the substrate along its entire length. The cord of one egg mass was laid straight, varied from 0.1 to 0.5 mm in diameter, and measured 20 mm in length. Two other egg masses were C-shaped, with the cord varying from 0.75 to 1.5 mm in diameter; one of these was 7 mm long, the other 10 mm.

Diaulula sandiegensis (Cooper, 1863)

This species is moderately common at Cape Arago and is often seen under ledges and boulders feeding on *Haliclona* sp. A of SMITH & CARLTON (1975:45). Specimens ranged in size from 5 to 70 mm. Specimens less than 15 mm were found in January, March, April, June, and July, and specimens over 50 mm long were found in May through July, and in October and January. Small to medium size individuals are often at the end of a "path" they have eaten into *Haliclona* sp. and, due to the resemblance of their dorsal brown rings or spots to the oscula of the sponge, are quite cryptic. One 40 mm specimen was found in April at North Cove feeding on a buff colored, encrusting species of *Sigmatocia*. This is a new food record for *Diaulula sandiegensis* (McDONALD & NYBAKKEN, 1978; BLOOM, 1981).

Dirona albolineata Cockerell & Eliot, 1905

This species was abundant at North Cove during the latter part of summer in 1980, 1981, and 1982. It was rare or absent in the other seasons I looked. In 1983 I did not see any until early September, when only two were found. *Dirona albolineata* is usually observed crawling on algae and rocks in pools along with *Janolus fuscus* and *Triopha catalinae*.

Discodoris heathi MacFarland, 1905

I found five specimens ranging in size from 7 to 90 mm during the summer months at North Cove, and one 20 mm individual in August at Middle Cove. An 11 mm specimen found embedded in *Mycale macginitiei* under a boulder ate this sponge in the laboratory. A 60 mm slug ate a 30 mm diameter *Mycale macginitiei* overnight. *Discodoris heathi* has been reported feeding on a number of species of *Mycale* but not *Mycale macginitiei* (McDONALD & NYBAKKEN, 1978; BLOOM, 1981).

Discodoris heathi lays large yellow egg masses in the typical dorid form.

Doto amyra Marcus, 1961

I observed this species only at Middle Cove: one specimen in July 1980, five in June 1981, and 22 (with egg masses) in May and July 1983.

Despite the taxonomic confusion surrounding eastern Pacific *Doto* species (MARCUS, 1961 described four new species, but BEHRENS, 1980 and McDONALD & NYBAKKEN, 1980 list only two of those), I am calling this species *Doto amyra* after McDONALD & NYBAKKEN (1980). With the exception of one, all the specimens I examined matched their description and photograph of *Doto amyra* (Marcus's original description mentions little about the living animal). The cerata cores varied from light yellow to light orange-brown; the gonads were yellow, and the cerata tubercles were translucent white and contained slightly opaque white grains (these grains are larger and less dense than the opaque white grains present in the distal parts of the rhinophores and their sheaths). The exceptional specimen mentioned above, while possessing all the above characteristics, also possessed a subcutaneous black pigment in the body similar to that in the body of *Doto kya*. However, this slug laid eggs identical to those of the other specimens of *Doto amyra*, and, as indicated below, the eggs of *Doto amyra* are very different from those of *Doto kya*.

Most of the specimens of *Doto amyra*, and all of the egg masses, were on colonies of the thecate hydroid *Abietinaria* sp., a previously reported prey of *Doto amyra* (BEEMAN & WILLIAMS, 1980). Slugs occurred on both the stolons and upright portions of the hydroid. Egg masses were usually attached to the bases of the colonies.

Doto amyra feeds on *Abietinaria* sp. by rasping a circular hole in the perisarc with its radula and then sucking out

the hydroid tissues by means of muscular contractions of its esophagus (personal observations). One 5 mm long slug rasped a hole 32 μ m in diameter in the perisarc.

Doto amyra lays yellowish egg masses that are laterally flattened, slightly crescent-shaped with rounded ends, and laid on edge. The thick jelly attachment sheet is translucent white with parallel white striations; the rest of the egg mass jelly is clear. Egg masses measure up to 1.5 mm high by 4 mm long and derive their yellow color from the yellow eggs.

The larvae of *Doto amyra* hatch out as crawling veligers possessing large eyespots, a large foot, a small velum, and poor swimming abilities. In the presence of *Abietinaria* sp., they metamorphose into juvenile slugs within a few days after hatching (personal observation). *Doto amyra* is the first eastern Pacific nudibranch known to produce lecithotrophic larvae (type 2 development of THOMPSON, 1967) (HURST, 1967; THOMPSON, 1967; BONAR, 1978; present study). I will examine this development more closely elsewhere (ms in preparation).

Doto kya Marcus, 1961

In May and June 1980 I found four specimens at North Cove. Two of these were among *Plumularia* sp. and a short unidentified hydroid of the family Campanulinidae. Both hydroids were growing on the perennial portion of the brown alga *Cystoseira*. Three more were seen at Middle Cove in July 1983. All specimens match the photograph of *Doto kya* in BEHRENS (1980).

The white egg masses of *Doto kya* are laterally flattened (more flattened than the egg masses of *Doto amyra*), slightly wavy or folded crescents to semi-circles; they are laid on edge and measure up to 3 mm in length.

Eubbranchus olivaceus (O'Donoghue, 1922)

Two specimens, 6 mm and 8 mm long, were found at North Cove in June and July 1983. The radula from the latter has 42 rows of teeth and does not taper. As MARCUS (1961:49) noted, the nontapering radula is at present the major anatomical character distinguishing *E. olivaceus* from *E. rustyus*.

Eubbranchus rustyus (MARCUS, 1961)

I found a few *Eubbranchus rustyus* in the summer months

at North and Middle coves. Six specimens 0.5–5 mm long occurred with egg masses on *Plumularia* sp. at Middle Cove in July 1983. *Eubbranchus rustyus* eats this hydroid in the laboratory (personal observation). The radula from a 6-mm long specimen has 57 rows of teeth and tapers distinctly.

Flabellina trilineata (O'Donoghue, 1921)

Flabellina trilineata is the most abundant eolid at Cape Arago and occurs at all four coves. It is commonly found feeding on *Tubularia marina*, an abundant hydroid at Cape Arago. Both species appear to be most abundant during the spring. I have observed *F. trilineata* feeding on *Eudendrium californicum* TORREY, 1902, in California, and McDONALD & NYBAKKEN (1978) report it feeding on *Eudendrium* sp. Although large *Eudendrium californicum* colonies occur at Middle Cove, often in close proximity to *F. trilineata* and *Tubularia marina*, I never observed the eolid on them. This suggests that *F. trilineata* prefers *Tubularia marina* to *Eudendrium californicum*.

Many individuals of *F. trilineata* lacked orange pigment on the rhinophores and cephalic tentacles. MACFARLAND (1966:321) also noted this variability in color pattern.

Hallaxa chani Gosliner & Williams, 1975

Since first reporting two specimens of *Hallaxa chani* from North Cove, Cape Arago (GODDARD, 1981), I have seen over 70 individuals in the North Cove inner boulder field, and as many as 14 specimens on a single low tide. *Hallaxa chani* is usually on or near its sponge prey *Halisarca* sp. underneath mid- to low-intertidal boulders (Figures 4, 5).

In the laboratory, specimens of *Hallaxa chani* of all sizes readily feed on *Halisarca* sp. and do not feed on the white colonial tunicate (either *Didemnum carnulentum* RITTER & FORSYTH, 1917, or *Trididemnum opacum* [RITTER, 1907]) that is common under North Cove boulders and was previously suspected to be eaten by *H. chani* (see GODDARD, 1981). I have never observed *H. chani* feeding on any other organisms.

Hallaxa chani blends well with *Halisarca* sp. (Figures 4, 5). Both organisms are light to yellowish-tan in color, and the reddish-brown flecks and subcutaneous dark spots on *H. chani* match the dark spots on *Halisarca* sp. (The

Explanation of Figures 2 to 6

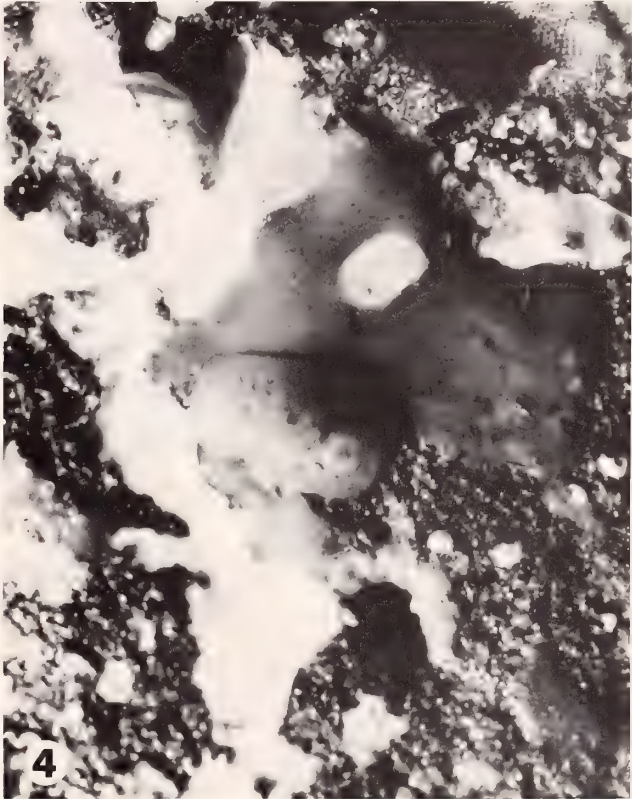
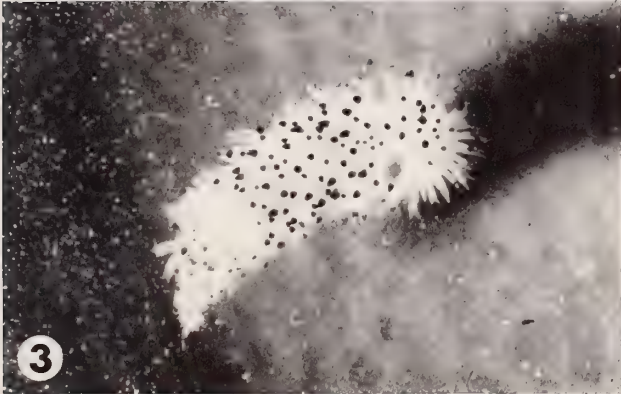
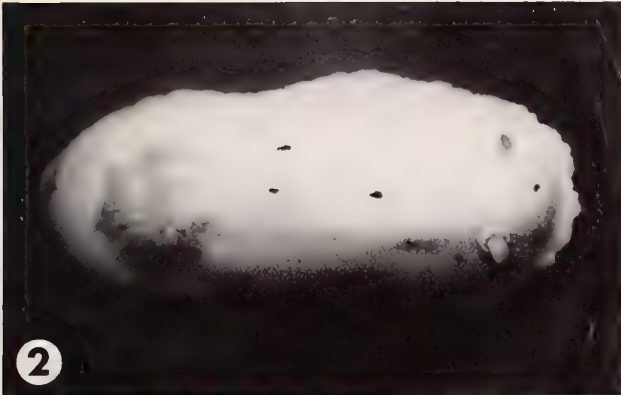
Figure 2. *Anisodoris lentiginosa*, about 90 mm long, found at Good Witch Cove on 18 May 1980.

Figure 3. *Crimora coneja*, 16 mm long, found at North Cove on 29 August 1981 by Kathryn Young and Tom Wayne.

Figure 4. *Hallaxa chani*, about 20 mm long, on *Halisarca* sp. on the underside of a North Cove boulder. 28 April 1982. Note the matching color pattern of the dorid and the sponge. The surrounding white organism is the colonial tunicate *Didemnum carnulentum*.

Figure 5. *Hallaxa chani*, about 18 mm long, on *Halisarca* sp. (center) on the underside of a North Cove boulder. 28 April 1982.

Figure 6. Same spot as in Figure 5, 13 days later. The specimen of *Hallaxa chani* in Figure 5 has eaten all of the *Halisarca* sp., deposited an egg mass, and moved on. 11 May 1982. The small egg mass above the egg mass of *Hallaxa chani* was laid by *Rostanga pulchra*. The sponge in the lower portion of this photograph is *Lissodendoryx firma*; it was subsequently eaten by *Anisodoris nobilis* (see text on *A. nobilis*).



"dark spots" on *Halisarca* sp. are caused by the sponge structure rather than pigmentation. They appear to be associated with the water canal system.) Moreover, when feeding, *H. chani* tends to spread out its semi-translucent dorsum, thus taking on some of the sponge color and also making the thin edge of the dorsum difficult to discern. Small *H. chani* are very cryptic.

Observations indicate that *Hallaxa chani* grows rapidly for a dorid of its size, reaches maturity in a few months, and lives approximately six months. One individual, 5 mm long (wet weight of 20 mg) at collection, kept in 10°C water and given *Halisarca* sp. every few weeks, grew to a wet weight of 360 mg in 44 days, and laid an egg mass 44 days after collection. It weighed 121 mg on day 132, and was moribund after 152 days. Four other specimens of similar initial weight (including one that was kept isolated and never laid eggs but which reached a length of 28 mm and a weight of 957 mg) lived 150 days or less under similar conditions.

The egg mass of *Hallaxa chani* is a cream colored ribbon 2–3 mm high laid in a loose spiral of 1 to 3 turns (Figure 6). The hatching veligers lack eyespots and possess type 1 shells whose oldest portion is a translucent brown color. Specimens of *H. chani* less than 5 mm long occurred in all seasons, and egg masses were found in all seasons except winter, indicating that reproduction occurs most of the year.

Hermaea vancouverensis O'Donoghue, 1924

I found four specimens, 6–8 mm long, of this sacoglossan on brown algae in the North Cove inner boulder field in June 1981.

Hermisenda crassicornis (Eschscholtz, 1831)

Hermisenda crassicornis was not very common at Cape Arago. In June 1981 I found over 20 specimens at Middle Cove, but on other occasions never more than six. Interestingly, *H. crassicornis* is abundant on the docks of the Charleston boat basin during spring and summer. Most of the *H. crassicornis* individuals at Cape Arago and the boat basin are the variety possessing a bluish-white stripe on the cerata (see BEHRENS, 1980:93, lower photograph). *Hermisenda crassicornis* occurs in all four coves.

Janolus fuscus O'Donoghue, 1924

GOSLINER (1982) recently reinstated *Janolus fuscus* as a distinct species from the more southerly *Janolus* (*Antiopella*) *barbarensis* (Cooper, 1863). Cape Arago *Janolus* are all *Janolus fuscus*, and the *Antiopella barbarensis* reported from Oregon by SPHON (1972) were undoubtedly also *J. fuscus*.

Janolus fuscus occurred from April to October at North Cove only. During August and September it is one of the most abundant and conspicuous nudibranchs at North Cove. It is usually found crawling on rocks or on the algae

Sargassum and *Egrelia* and the surfgrass *Phyllospadix* in the large pools of the inner boulder field where it searches for the arborescent bryozoans upon which it feeds (MCDONALD & NYBAKKEN, 1978; personal observation).

Laila cockerelli MacFarland, 1905

Laila cockerelli was uncommon at Cape Arago until spring and summer 1983 when I found a total of 20 specimens at North and Middle coves. It also occurs at South and Good Witch coves. A number of individuals were observed on the light orange bryozoan *Hincksina velata* (Hincks, 1881) and ate this bryozoan in the laboratory. *Laila cockerelli* has been reported feeding on *Hincksina velata* in California (MCDONALD & NYBAKKEN, 1978).

My observations of the pink colored egg mass of *Laila cockerelli* generally match those of O'DONOGHUE & O'DONOGHUE (1922). However, they described it as a "slightly flattened string . . . wound in a close, tight-fitting spiral." Egg masses I observed were a ribbon laid flat in a close spiral. It is very similar in morphology to the egg mass of *Crimora coneja*. One egg mass had 4.5 turns, a diameter of 15 mm, and a ribbon whose width varied from 1.5 to 2.0 mm.

Onchidoris muricata (Müller, 1776)

Onchidoris muricata occurred at North Cove only. I observed specimens in spring 1980, from late summer 1981 to early spring 1982, and again in spring 1983. On two occasions (December 1981 and January 1982) I found over ten specimens; on all other trips six or fewer were seen.

Onchidoris muricata usually occurs under boulders on *Eurystomella bilabiata* (Hincks, 1884) or *Microporella criboosa* (Osburn, 1952), two abundant ascophoran bryozoans which it eats in the laboratory (personal observation). *Onchidoris muricata* that have been feeding on *Eurystomella bilabiata* possess a deep red colored digestive gland visible through the foot. I also found *O. muricata* on *Hincksina minuscula* but did not confirm feeding on this species.

Onchidoris muricata can be difficult to distinguish from *Adalaria* sp. in the field. However, *O. muricata* is usually shorter, rounder, and has bulbous, fairly smooth dorsal papillae. The pointed spicules in the papillae of *O. muricata* barely protrude above the surface of the papillae; those of *Adalaria* sp. protrude very far.

HURST (1967) described the egg mass of *Onchidoris muricata*. Like many other dorids, *O. muricata* sometimes lays only a small portion of an egg coil (personal observation).

Onchidoris sp. (cf. *Onchidoris hystricina*)

This species is referred to as *Onchidoris hystricina* by BEHRENS (1980:66–67), MCDONALD & NYBAKKEN (1980:

44–45), BEEMAN & WILLIAMS (1980:328), and McDONALD (1983:198–199). However, *Onchidoris* sp. disagrees with BERGH's 1878 and 1880 descriptions of *O. hystricina*, as well as MARCUS's (1961) description of *O. hystricina*. The dorsal papillae, gills, and radula are very different (Sandra Millen, personal communication; personal observation). The species appears to be undescribed.

Onchidoris sp. was observed only at North Cove and only at the end of summer. I found ten in August 1981, seven in August and September 1982, and six in August and September 1983.

The white egg mass of *Onchidoris* sp. is a cord, 0.75–1.0 mm in diameter, laid in a disorderly spiral of 1 to 4 turns measuring up to 5 mm in diameter.

Placida dendritica (Alder & Hancock, 1843)

I found this species feeding on *Codium fragile* in pools between South and Good Witch coves. BEHRENS (1980) reports San Francisco Bay as the northern limit of this species, but LAMBERT (1976) found it on the northern tip of Vancouver Island, British Columbia.

Polycera atra MacFarland, 1905

Three specimens were observed in September 1983 at North Cove. *Polycera atra* occurred by the hundreds feeding on arborescent bryozoans in the Charleston boat basin in June 1983, but repeated observation in mid-July turned up only a single specimen. The range of *Polycera atra* is extended from Humboldt Bay, California (JAECKLE, 1981).

Precuthona divae Marcus, 1961

This eolid occurred in low numbers at North and Middle coves in the spring and summer. One specimen from Middle Cove was 32 mm long. I have also found *Precuthona divae* at Cape Blanco (50 km south) feeding on the pink colonies of *Hydractinia* sp. The egg mass of *P. divae* is a round, hemispherical rosette. ROBILLIARD (1971b) reported egg masses of *P. divae* from San Juan Island, Washington, as being white; those at my study sites were pink.

Rostanga pulchra MacFarland, 1905

Rostanga pulchra is abundant at Cape Arago and occurs with its egg masses throughout the year. I observed it feeding on *Ophlitaspongia pennata* and also found it (and its eggs) on *Antho lithophoenix* (de Laubenfels, 1927) and *Hymedesmia* sp. A (of SMITH & CARLTON, 1975:51). I also found *R. pulchra* close to, but not on, *Plocamia karykina* de Laubenfels, 1927, and *Axocelita originalis* (de Laubenfels, 1930). *Rostanga pulchra* has previously been reported feeding on, or occurring on, all of the above sponges except for *Hymedesmia* sp. A (McDONALD & NYBAKKEN, 1978).

Triopha catalinae (Cooper, 1863)

One of the most common dorids at Cape Arago, *Triopha catalinae* occurs year-round but is most abundant during summer and fall, especially at North Cove. Individuals ranging in size from less than 10 mm to 70 or 80 mm can be found in nearly any month; this suggests a long breeding season and a probable lack of synchrony of reproduction among individuals. I have never seen *T. catalinae* egg masses in the field. Egg masses laid in aquaria are large, pinkish-white, coiled ribbons laid on edge.

At Cape Arago *Triopha catalinae* feeds on unidentified species of arborescent and encrusting bryozoans. Small individuals are often found on bryozoans on the undersides of boulders, and large individuals are usually out in the open, crawling on submerged algae and rocks.

Triopha maculata MacFarland, 1905

I found five orange specimens during summer 1983 at North Cove. All were 10–20 mm long, and three were observed on bryozoans underneath boulders.

Tritonia festiva (Stearns, 1873)

Tritonia festiva occurs at all four coves but is most common at Middle and Good Witch coves. It usually occurs on or near a white to salmon colored alcyonacean octocoral upon which it feeds. SOWELL (1949) also reported finding *T. festiva* "on or near" this octocoral but did not confirm feeding. The octocoral is in the form of low, rounded colonies up to 15 mm in diameter and is undescribed (F. M. Bayer, personal communication). Large aggregations of fairly evenly spaced colonies are common under wave-exposed, low-intertidal ledges at Cape Arago.

The feeding of *Tritonia festiva* on the soft coral is remarkable. The following description is based on observations of 20 feeding attacks made by *T. festiva* 15–25 mm long on soft coral colonies 7–10 mm in basal diameter. While searching for its prey the frontal veil of *T. festiva* is laterally expanded and horizontal. Upon contacting an expanded colony with the sensitive, slender processes on its frontal veil (or with its rhinophores), *T. festiva* pulls back its head, slows its crawling, raises the frontal veil, and begins eversion of its oral canal. The slug crawls slowly and carefully forward, using the tactile sense of the frontal veil and oral canal to position the expanded oral canal over the end of one or a few polyps. Polyps touched by the frontal veil and oral canal contract their tentacles but not their stalks. Once positioned, *T. festiva* rapidly thrusts its head forward while extending its buccal mass. The jaws and radula make a number of strikes in rapid succession, and one to seven polyps are ripped out of the colony as the rest of the polyps quickly contract. Ingested polyps can be seen passing through the esophagus immediately following an attack. *Tritonia festiva* will not attack contracted colonies, probably because they cannot

penetrate the tough and densely spiculate coenenchyme. Every attack I observed was successful.

This feeding process is similar to that described by THOMPSON (1976) for *Tritonia hombergi* Cuvier feeding on *Alcyonium digitatum* (Linnaeus) and is also quite similar (particularly in the positioning phase) to the feeding sequence described by WILLOWS (1978) for *Tritonia diomedea* Bergh, 1894, feeding on the sea pen *Virgularia* sp. *Tritonia hombergi* and *T. diomedea* attain much larger size than *T. festiva* and bite off and ingest pieces of coenenchyme and sections of sea pen respectively. I have observed *T. festiva* biting off only polyps. Large *T. festiva* (or *T. festiva* feeding on small colonies) may bite off pieces of coenenchyme or ingest small colonies.

Tritonia festiva also occurred next to *Clavularia* sp., a stoloniferan octocoral that I observed *T. festiva* eating in the laboratory and which has previously been reported as a prey item of *T. festiva* (MCDONALD & NYBAKKEN, 1978). *Tritonia festiva* from Cape Arago also attacked specimens of *Gersemia rubiformis* (Pallas, 1788) collected from Cape Blanco as well as an unidentified pink gorgonian dredged offshore by local fishermen.

The white egg mass of *Tritonia festiva* is a flattened cord laid in a close spiral and attached to the substrate by a thin, egg-free jelly sheet (type B egg mass of HURST, 1967). The cord is somewhat convoluted, giving the egg mass a rosette appearance. Dimensions are: egg mass diameter, 10–20 mm; height, 1 mm; cord diameter, 0.5 mm. The egg mass is delicate, and the egg capsules are not embedded in a jelly matrix.

DISCUSSION

Life Cycles

Most of the dorid nudibranchs, and all of the eudoridaceans, whose life cycles have been studied have been shown to possess annual life cycles (SWENNEN, 1961; MILLER, 1962; THOMPSON, 1964, 1976; POTTS, 1970; CLARK, 1975; TODD, 1978, 1979; EYSTER & STANCYK, 1981). Dorids known or suspected to possess subannual life cycles are generally smaller, bryozoan-feeding members of the families Corambidae, Goniadorididae, and Polyceridae and the genus *Acanthodoris* (SWENNEN, 1961; MILLER, 1962; CLARK, 1975; PERRON & TURNER, 1977).

Data presented above on the lifespan of *Hallaxa chani* strongly suggest that this eudoridacean is subannual. Combining the observations on lifespan, egg-laying, and larval development, and assuming a one-month planktonic existence and one or two months for the juvenile to reach a length of 5 mm, the generation time appears to be about four or five months at 10°C. It could be shorter at higher temperatures.

The relatively rapid growth and short generation time of *Hallaxa chani* appear to be adaptations for exploiting its sponge prey *Halisarca* sp. A species of *Halisarca* from New Zealand grows rapidly compared to most other sponges and has a generation time of four to five months

(BERGQUIST, 1978). I observed one group of *Halisarca* sp. individuals under a marked boulder at Cape Arago increase in area from 8 cm² to 16 cm² between 29 June 1983 and 7 September 1983 (70 days), and I cannot rule out the possibility that they were preyed upon during this period and thus actually grew more. The North Cove *Halisarca* sp. population is composed of widely distributed individuals averaging only a few square centimeters in area (personal observation). Laboratory and field observations indicate that specimens of *Hallaxa chani* are capable of eating these individuals in a matter of days to weeks (Figures 5, 6).

It is tempting to postulate that natural selection has "traded" spicule production in both *Halisarca* sp. and *Hallaxa chani* for faster growth rates. However, the lack of spicules in *Hallaxa chani* may be adaptive primarily in conferring a textural resemblance to *Halisarca* sp., helping to camouflage the dorid from its predators (GODDARD, 1981). Lacking spicules, *Halisarca* sp. probably has chemical defenses against sponge predators (it does have a pungent odor when torn). Of course, if such defenses do exist in *Halisarca* sp., *Hallaxa chani* and *Cadlina modesta* have been able to overcome them and possibly even use them in their own defense.

Observations on the longevity of *Cadlina luteomarginata* and *Cadlina modesta* suggest that these dorids live at least a year, and thus possess life cycles similar to those known for other eudoridaceans. One *Cadlina modesta* survived a period of starvation longer (and at higher temperatures) than the entire lifespan of regularly fed *Hallaxa chani*. Although this *Cadlina modesta* never laid eggs, observations by THOMPSON (1961), TODD (1978), and EYSTER (1981), as well as the above observations on one *Hallaxa chani* that never laid eggs, all indicate that lack of reproduction can result in larger size, but does not significantly affect lifespan.

Development

Data on the larval development of Cape Arago opisthobranchs are summarized in Table 1. *Aplysiopsis smithi*, *Onchidoris muricata*, and *Triopha catalinae* are the only species in this table whose development has previously been examined (HURST, 1967; GREENE, 1968; BEEMAN & WILLIAMS, 1980).

The development times, egg and veliger sizes, and the production of veligers that lack a propodium, usually lack eyespots, and possess a mantle fold that attaches intermittently to the shell lip all indicate that, with the exception of *Doto amyra*, every species in Table 1 produces planktotrophic veliger larvae (type 1 development of THOMPSON, 1967) (THOMPSON, 1967, 1976). As mentioned previously, *Doto amyra* produces lecithotrophic veligers (type 2 development).

Of the 20 species in Table 1 that produce planktotrophic larvae, four (20%) produce veligers possessing eyespots at hatching. This is rather high considering that the ve-

Table 1
Larval development of Cape Arago opisthobranchs.

Species	Diameter of ova (μm)			Ova per capsule	Embryonic period (days)	Culture temp. ($^{\circ}\text{C}$)	Shell type ⁴	Length of veliger shell ⁵ (μm)		Eye-spots at hatching
	Range ¹	Month ²	N ³					Range ¹	N ³	
<i>Adalaria</i> sp.	81.2–83.7	April	3	1	11	10–12	1	136.0–143.5	3	no
<i>Ancula pacifica</i>	58.3–59.0	June	2	1	9	14–16	1	103.8	1	no
<i>Anisodoris nobilis</i>	83.0	June	1	up to 20	14	14–17	1	152.8	1	no
<i>Aplysiopsis smithi</i>	66.0	July	1	1	7	15–17	1	112.9	1	no
<i>Berthella californica</i>	92.6	May	1	1–2	18	11–14	1	152.7	1	yes
<i>Cadlina modesta</i>	91.0–92.0	April	3	1	16–19	12–15	1	155.6–158.4	4	no
<i>Catriona columbiana</i>	99.7	July	1	1	10	15–17	2	273.9	1	yes
<i>Crimora coneja</i>	71.6–74.2	April	3	1	17–18	10–14	1	115.5–123.5	3	no
<i>Cuthona cocoachroma</i>	96.3	July	1	1	6	15–17	2	256.7	1	no
<i>Diaphana californica</i>	73.2	Sept.	1	1	7–8	12–16	1	122.1–123.6	2	no
<i>Discodoris heathi</i>	76.8	June	1	4–7	15	14–17	1	144.8	1	no
<i>Doto amyra</i>	149.6–154.3	May	4	1	19–21	15–17	1	236.0–238.5	2	yes
<i>Doto kya</i>	~75	July	1	1	7	15–17	1	122.3	1	no
<i>Eubranchius rusticus</i>	92.9	July	1	1	6	15–17	2	240.1	1	yes
<i>Hallaxa chani</i>	79.6–82.6	May	4	1	15–17	11–15	1	147.9–154.1	3	no
<i>Laila cockerelli</i>	95.4	April	1	1	17	10–13	1	141.8	1	no
<i>Onchidoris muricata</i>	75.0–77.3	April	2	1	10–11	7–11	1	128.5–135.6	3	no
<i>Onchidoris</i> sp.	62.6–64.0	Sept.	4	1	9–11	12–16	1	113.3–116.6	4	no
<i>Precuthona divae</i>	107.1	July	1	1	8	15–17	2	249.1	1	no
<i>Triopha catalinae</i>	—	Aug	1	1	10	14–18	1	~130	1	no
<i>Tritonia festiva</i>	78.9	June	1	1	12	14–17	1	125	1	yes

¹ Range of means. Means calculated from measurements (usually ten) of ova (or veliger shells) from a single egg mass.

² Month in which egg masses laid.

³ N = number of egg masses in which ova (or veliger shell lengths) were measured.

⁴ See HURST (1967).

⁵ Length = longest dimension of shell.

ligers of only one of the 30 northeastern Pacific opisthobranchs studied by HURST (1967) has eyespots at hatching and the statement by THOMPSON (1976) that hatching planktotrophic veligers usually lack eyespots. Planktotrophic veligers develop eyespots before metamorphosis, and species with lecithotrophic or direct development always possess eyespots at hatching (THOMPSON, 1976). As BONAR (1978:187) states "the eyes . . . usually develop rather late in embryogenesis, and along with the appearance of an enlarged propodium signal the approach of metamorphic competence." It thus seems likely that the above four species will be found to possess relatively short obligatory planktonic stages compared to many other species with planktotrophic larvae.

The data in Table 1 generally support THOMPSON's (1976:86) generalization that "within development-type 1, species with the largest eggs have a longer embryonic period, and, moreover, give rise to larger veliger larvae."

Food, Competition, and Aggression

Although most nudibranch species are known to eat a number of prey species (THOMPSON, 1964, 1976; McDONALD & NYBAKKEN, 1978), a few species appear to be monophagous over their entire ranges. Of the species found

at Cape Arago, *Adalaria* sp., *Ancula pacifica*, *Hallaxa chani*, *Laila cockerelli*, and *Precuthona divae*, so far as is known, fit into this latter category (McDONALD & NYBAKKEN, 1978; BEEMAN & WILLIAMS, 1980; GODDARD, 1981; present study). *Crimora coneja* apparently feeds only on *Hincksia minuscula* at Cape Arago, but it is doubtful that this bryozoan occurs in San Diego County, California, one of the other locations where *C. coneja* occurs (OSBURN, 1950). The generalist species at Cape Arago appear to include *Anisodoris nobilis*, *Dirona albolineata*, *Hermisenda crassicornis*, *Rostanga pulchra*, and *Triopha catalinae* (ROBILLIARD, 1971a; NYBAKKEN & EASTMAN, 1977; McDONALD & NYBAKKEN, 1978; BEEMAN & WILLIAMS, 1980; BLOOM, 1981; JAECKLE, 1984; present study). I suspect that most nudibranch species will be found to eat relatively few prey species belonging to a few genera. Data obtained in this study on the prey of Cape Arago nudibranchs are summarized in Table 2. These data are incomplete. With the possible exceptions of *Cadlina modesta*, *Crimora coneja*, and *Hallaxa chani*, more data are needed on the prey of all Cape Arago nudibranchs.

Food data presented in Table 2 for *Anisodoris nobilis*, *Archidoris montereyensis*, *Archidoris odhneri*, *Diaulula sandiegensis*, and *Discodoris heathi* generally agree with data presented by BLOOM (1981, table 2) on the order of sponges

Table 2

Prey of Cape Arago opisthobranchs.

	Prey
Nudibranch species	
<i>Adalaria</i> sp.	<i>Hincksina minuscula</i> *
<i>Aeolidia papillosa</i>	<i>Epiactis prolifera</i>
<i>Ancula pacifica</i>	among <i>Barentsia</i> sp.
<i>Anisodoris nobilis</i>	<i>Mycale macginitiei</i>
	<i>Zygherpe hyaloderma</i>
	<i>Lissodendoryx firma</i>
	<i>Tedania gurjanovae</i> *
	<i>Ophlitaspongia pennata</i> (Lab)*
<i>Archidoris montereyensis</i>	<i>Halichondria panicea</i>
	<i>Suberites</i> sp.
	unidentified orange encrusting sponge
<i>Archidoris odhneri</i>	<i>Hymeniacidon ungodon</i> *
	on <i>Suberites</i> sp.
<i>Cadlina luteomarginata</i>	<i>Aplysilla glacialis</i> *
	<i>Halisarca</i> sp. (Lab)*
<i>Cadlina modesta</i>	<i>Aplysilla glacialis</i>
	<i>Halisarca</i> sp.*
<i>Catriona columbiana</i>	<i>Tubularia marina</i>
<i>Crimora coneja</i>	<i>Hincksina minuscula</i> *
<i>Cuthona abronia</i>	among small thecate hydroids
<i>Cuthona albocrusta</i>	among small thecate hydroids
<i>Dendronotus frondosus</i>	<i>Obelia</i> sp.
<i>Diaulula sandiegensis</i>	<i>Haliclona</i> sp. A
	<i>Sigmatocia</i> sp.*
<i>Discodoris heathi</i>	<i>Mycale macginitiei</i> *
<i>Doto amyra</i>	<i>Abietinaria</i> sp.
<i>Doto kya</i>	among <i>Plumularia</i> sp. and small thecate hydroids
<i>Eubranchius rustyus</i>	<i>Plumularia</i> sp.
<i>Flabellina trilineata</i>	<i>Tubularia marina</i>
<i>Hallaxa chani</i>	<i>Halisarca</i> sp.
<i>Janolus fuscus</i>	arborescent bryozoans
<i>Laila cockerelli</i>	<i>Hincksina velata</i>
<i>Onchidoris muricata</i>	<i>Eurystomella bilabiata</i> *
	<i>Microporella cribosa</i> *
	on <i>Hincksina minuscula</i>
<i>Polycera atra</i>	arborescent bryozoans
<i>Precuthona divae</i>	<i>Hydractinia</i> sp.
<i>Rostanga pulchra</i>	<i>Ophlitaspongia pennata</i>
	on <i>Antho lithophoenix</i>
	on <i>Hymedesmia</i> sp. A
	near <i>Plocamia karykina</i>
	near <i>Axocelita originalis</i>
<i>Triopha catalinae</i>	arborescent bryozoans
<i>Triopha maculata</i>	arborescent and encrusting bryozoans
<i>Tritonia festiva</i>	undescribed alcyonacean octocoral*
	<i>Clavularia</i> sp.
	<i>Gersemia rubiformis</i> (Lab)

Table 2 (Continued)

	Prey
Sacoglossan species	
<i>Aplysiopsis smithi</i>	<i>Cladophora</i> sp.
<i>Placida dendritica</i>	<i>Codium fragile</i>

* New food record.

(Lab) opisthobranch species not found associated with this prey in field, but ingestion of prey observed in laboratory.

most frequently eaten by these dorids in the San Juan Archipelago and further support his general conclusion that "caecate dorids prey on sponges with poorly-organized skeletons and acaecate dorids prey on sponges with well-organized skeletons."

The Cape Arago populations of a number of nudibranchs are clearly not food limited. For example, *Adalaria* sp., *Crimora coneja*, *Laila cockerelli*, and *Onchidoris muricata* all feed on encrusting bryozoans that are abundant at Cape Arago year-round (personal observation), but the nudibranchs themselves are either rare or only sporadically common. It is not known what factors are preventing these species from becoming more abundant. On the other hand, populations of *Cadlina modesta* and *Hallaxa chani* (and *Flabellina trilineata* during periods of high abundance) appear to be much closer to being limited by the abundance of their food. *Aplysilla glacialis* and *Halisarca* sp. are quite scarce; the abundance of *Tubularia marina* fluctuates markedly, possibly as a result of eolid predation.

Large numbers of *Triopha catalinae*, *Janolus fuscus*, and *Dironea albolineata* are found together in the North Cove inner boulder field during late summer and early fall. *Triopha catalinae* and *J. fuscus* feed on arborescent bryozoans (NYBAKKEN & EASTMAN, 1977; McDONALD & NYBAKKEN, 1978; personal observation), and *D. albolineata* eats a wide variety of prey including bryozoans (ROBILLIARD, 1971a). It seems likely that some competition for food occurs between these species during periods of co-occurrence.

When *Janolus fuscus* are crowded in the laboratory they often bite each other, sometimes tearing off and ingesting cerata (Katheryn Young, personal communication; personal observation). I have also observed *Tritonia festiva* taking bites out of each other in the laboratory. In one instance I placed two newly collected specimens of *Tritonia festiva* (20 mm and 35 mm long, collected in June) together in 500 mL of water. Within one day the larger had eaten the smaller specimen. The occurrence of this aggressive behavior and cannibalism has not been documented for either species in the field. It is interesting to note, however, that aggressive behavior between *Tritonia festiva* could be adaptive in reducing feeding interference. As mentioned previously, the alcyonacean prey of Cape

Arago *Tritonia festiva* often occurs in large aggregations of closely and evenly spaced colonies. A feeding attack by *Tritonia festiva* on a colony results in contraction of the remaining polyps of that colony for about two days (personal observation). *Tritonia festiva* will not attack contracted colonies. Feeding interference between *Tritonia festiva* could thus be considerable at high slug densities (*i.e.*, most of the colonies would be contracted). Aggressive behavior between *Tritonia festiva* might be a mechanism for reducing slug density and thus feeding interference.

In *Hermissenda crassicornis*, biting of conspecifics usually follows "sidling" behavior (ZACK, 1975; RUTOWSKI, 1982). Recent work has shown that sidling behavior is actually "alignment for copulation" (LONGLEY & LONGLEY, 1982; RUTOWSKI, 1983). If not simply an attempt to obtain food, the function of the biting that immediately follows mating is obscure. It is possible that biting of conspecifics is also closely related to mating in *Janolus fuscus* and *Tritonia festiva*. Further studies of cannibalism and intraspecific aggression in these species and their relationship to slug density, food density, and size and reproductive state of the slugs are needed.

Triopha catalinae individuals are rarely found in close proximity to one another (NYBAKKEN & EASTMAN, 1977: 282; personal observation), suggesting that aggressive interactions may also occur between individuals of this species. The feeding method of *T. catalinae* (in which whole branches of arborescent bryozoans are ripped off and ingested), and the laboratory observation of a large *T. catalinae* attacking and taking a sizable bite out of a *Laila cockerelli* (personal observation) indicate that *T. catalinae* is physically capable of such aggression. Furthermore, one wonders whether interspecific aggression or predation may occur between *T. catalinae*, *Janolus fuscus*, and *Dirona albolineata*.

Ranges

The range extensions reported above for *Cuthona flavovulta*, *C. fulgens*, and *Polycera atra*, and the occurrence in spring and summer 1983 of the form of *Ancula pacifica* common in California may be related to events associated with the strong El Niño of 1982–1983 (PHILANDER, 1983). These events included above-normal ocean temperatures off the coast of North America (K. T. Briggs, Univ. of California, Santa Cruz, personal communication; A. McGee, Oregon Dept. Fish and Wildlife, personal communication) and probably a weakening and partial reversal of the usually south-moving California current (CHELTON, 1981), as well as an intensification of the near-shore, north-moving Davidson current that occurs in late fall and early winter (BOLIN & ABBOTT, 1963; SCHWARTZLOSE & REID, 1972). If the above species were transported north (as veligers) with these anomalous events, their occurrence at Cape Arago may be brief. On the other hand, they may occur relatively consistently, but in low numbers, at Cape Arago and were previously over-

looked—this appears to be the case for *Crimora coneja*, *Cuthona cocoachroma*, and *Diaphana californica*, all of which were found at Cape Arago before the onset of the above anomalous conditions.

I would like to recommend that dates of observation always be given with range extensions and reports of unusual occurrence. For with increasing monitoring and understanding of coastal hydrographic conditions, it may become possible to explain better the occurrence of many species at the edges of their ranges, or to explain why a species appears in an area for a time and then disappears for long periods. For example, is it possible that the specimens of *Hopkinsia rosacea* reported from Oregon by STEINBERG (1963b) (see below) were carried north (as veligers) from California with the warm waters and currents associated with the intense El Niño of the late 1950's? Mention of the date of observation would have helped evaluate such a possibility. It is interesting that *Eurystomella bilabiata*, the only known prey of *H. rosacea*, is abundant at Cape Arago year-round, but *H. rosacea* is usually absent (personal observation).

The known range of *Crimora coneja* is puzzling. Despite extensive field observation of nudibranchs in central California, only one specimen has been reported between San Diego and Cape Arago (MCDONALD, 1983).

Some Thoughts on the Effects of Nudibranch Predation on the Encrusting Animal Community at Cape Arago

Low-light habitats at Cape Arago (crevices, caves, and the undersurfaces of boulders and ledges) support a diverse encrusting community composed primarily of sponges, bryozoans, colonial tunicates, and cnidarians. The amount of free space varies depending, in part, on the habitat and degree of physical disturbance. For example, the undersurfaces of low intertidal ledges and stable boulders exposed to little sedimentation tend to have little free space, whereas the undersurfaces of boulders exposed to seasonal sedimentation and overturning by waves tend to possess large amounts of free space (personal observation).

As in any community, part of the encrusting animal diversity at Cape Arago can be explained by the spatial complexity of the habitats, coupled with niche diversification and the evolution of habitat selection. However, the coexistence of large numbers of species on relatively uniform surfaces suggests that other factors must be involved in regulating species diversity. Factors that have been implicated in affecting the diversity of other communities and that are probably important at Cape Arago include: predation and disease, fluctuations in the physical and biotic environments, physical disturbance in the forms of sedimentation, boulder-overturning by surf, and erosion (boring clams play a major role in erosion and production of spatial complexity at Cape Arago), and the existence of competitive networks among the encrusting species (CONNELL, 1972, 1978; DAYTON, 1971; HUSTON, 1979;

HUTCHINSON, 1961; JACKSON & BUSS, 1975; PAINE, 1974; SOUSA, 1979). The first three factors can maintain relatively high levels of diversity by preventing competitive equilibrium (at which time competitively inferior species are excluded from the community) from being reached. Of course, at high enough levels, these same factors can keep diversity low. The existence of complex competitive networks can increase the time necessary for competitive exclusion to occur or it could mean that major competitive dominants simply do not exist in the community (JACKSON & BUSS, 1975; JACKSON, 1979; KARLSON & JACKSON, 1981). As CONNELL (1978) and HUSTON (1979) have discussed, a number of these factors probably operate simultaneously in any particular community, with the relative importance of each factor varying in different communities. The observed diversity in a community is, thus, the result of a "dynamic equilibrium" between the growth rates of the component populations and the rates of the above mentioned factors (HUSTON, 1979).

Nudibranchs, which are known to be important predators in some encrusting communities (BLOOM, 1981; CLARK, 1975; DAYTON *et al.*, 1974; RYLAND, 1970; THOMPSON, 1964; and, on the basis of abundance, NYBAKKEN, 1974, 1978), appear to be among the most abundant and important predators of encrusting organisms at Cape Arago (personal observation). Other significant predators of these organisms at Cape Arago include prosobranchs such as *Diodora aspera* (Rathke, 1833) and members of the family Lamellariidae, and probably various chitons, asteroides, and fish (MORRIS *et al.*, 1980; personal observation). Certain flatworms, polychaetes, crustaceans, and pycnogonids are known to eat encrusting animals (MORRIS *et al.*, 1980) and may also be important, especially with regard to predation on newly settled organisms.

Not knowing which encrusting species are competitively dominant at Cape Arago, I cannot say to what extent nudibranchs prey on such species. But, because nudibranchs can eat large amounts of sessile organisms (see data on *Anisodoris nobilis*, *Cadlina luteomarginata*, *C. modesta*, *Crimora coneja*, *Discodoris heathi*, and *Hallaxa chani*) and eat such a wide variety of prey, many of which are among the more abundant species (personal observation), they undoubtedly significantly affect the competitive relationships in the encrusting community at Cape Arago. Some examples of their effects follow.

Other than reducing the abundance of their prey, the most obvious result of nudibranch predation on encrusting communities is the creation of free space available for larval recruitment or intrusion by surrounding organisms. By consuming entire individuals or colonies, nudibranchs can also alter the species composition under a boulder or ledge.

Overgrowth is one of the primary mechanisms of competition between encrusting organisms (JACKSON, 1979). In some cases nudibranchs (and other predators) can erase overgrowth events between encrusting species by preying

on the overgrowing species. This applies to sessile organisms that can be completely grazed off the overgrown species (*i.e.*, certain sponges, tunicates, and perhaps fleshy bryozoans). The sponge *Halisarca* sp. frequently overgrows the bryozoan *Eurystomella bilabiata* at Cape Arago. I have also seen it overgrowing the alcyonacean octocoral prey of *Tritonia festiva*. Twice I have collected *Eurystomella bilabiata* overgrown by *Halisarca* sp. in order to feed the sponge to laboratory *Hallaxa chani*. The dorids grazed the sponge cleanly off the bryozoan, and within a day or two the bryozoan lophophores were extended and feeding. Of course, the viability of the overgrown organism will depend on how long and how extensively it has been overgrown and on its sensitivity to any allelopathic substances made by the overgrowing organism. The large individual of *Aplysilla glacialis* I observed eaten by *Cadlina luteomarginata* and *C. modesta* (see notes on *C. luteomarginata*) had partially overgrown some *Cliona celata* Grant, 1826. The *Cliona celata* appeared healthy after the *Aplysilla* had been grazed away. This is not too surprising, however, considering the shell-boring abilities of *Cliona*; it also suggests that *Aplysilla glacialis* has little or no allelopathic effect on *Cliona celata*.

Partial predation, which results in decreased feeding and reproductive abilities of the grazed organism and can also expose it to settlement by possibly superior competitors (JACKSON & PALUMBI, 1979), is probably widespread. It is inevitable in spatially complex microhabitats where predators cannot reach all of their prey. Moreover, how many predators, given the chance, actually graze all of a sponge or every bryozoan zooid? Some predators are simply not capable of consuming entire colonies (*e.g.*, *Tritonia festiva* feeding on alcyonacean octocorals, and many hydroid-eating eolids that consume the hydranths, but not the stalks and stolons from which hydranths can regenerate). An important question is, how much can a sessile organism lose to predation and still survive with its regenerative abilities?

The feeding of *Tritonia festiva* on alcyonacean octocorals is a vivid example of partial predation. I have observed octocoral colonies being overgrown by *Halisarca* sp., colonial tunicates, and the "social" tunicate *Metandrocarpa taylora* Huntsman, 1912. It would be interesting to compare overgrowth of the octocoral in the presence and absence of *Tritonia festiva*.

The small, abundant dorid *Rostanga pulchra* feeds on the upper layers of orange sponges (personal observation) and appears to be more parasitic than predatory (though more data are needed on its movements, feeding rates, and sponge growth rates). By damaging the sponge, such superficial grazing may increase the sponge's susceptibility to overgrowth or may speed overgrowth interactions already begun. On the other hand, such feeding could possibly facilitate release of allelopathic chemicals and thus slow or prevent overgrowth.

The possible significance of the relationship between nudibranchs and the encrusting community is suggested

in a photograph I have of about 60 cm² of boulder undersurface. The area is completely covered by the bryozoans *Eurystomella bilabiata* and *Hincksina velata* and the sponge *Zygherpe hyaloderma*. Two clumps of an unidentified arborescent bryozoan are growing on the *Hincksina*. *Eurystomella* and *Hincksina* are overgrowing each other in different parts of the area, and the sponge is overgrowing *Hincksina*, but the sponge is also being overgrown by *Eurystomella*. Each of these organisms has at least one nudibranch predator at Cape Arago.

The competitive relationships between encrusting organisms can be very complex. Overgrowth outcomes vary between the same two species and often depend on encounter angle (JACKSON, 1979). Overgrowth may not be complete and certainly does not always result in mortality. Moreover, growth, regeneration, and recruitment rates of the encrusting species all can affect the observed diversity (KARLSON & JACKSON, 1981). If one adds predation (complete and partial) by organisms such as nudibranchs to this already complex system, as well as the other factors affecting diversity previously mentioned, one is left with an extraordinarily complex community for which competitive equilibrium seems unlikely. Rather, there is probably a "dynamic equilibrium," changing on both long and short time scales, between the rates of competitive displacement and the rates at which the other factors act to prevent competitive exclusion (HUSTON, 1979). The observed diversity of intertidal encrusting organisms at Cape Arago results from this dynamic equilibrium and is undoubtedly higher than would exist under a state of competitive equilibrium.

Benthic Opisthobranchs Known from Oregon

The 66 benthic opisthobranch species presently known from Oregon are listed in Table 3. Forty-seven of these have been found at Cape Arago. Twenty-six are new records for Oregon, and 28 are new to Cape Arago. The ranges of *Adalaria* sp. and *Anisodoris lentiginosa* are extended southward, and those of *Crimora coneja*, *Cuthona cocoachroma*, *C. flavovulta*, *C. fulgens*, *Diaphana californica*, and *Polycera atra* northward. Depending on the status of the questionable species listed in Table 3 (see below), the Oregon total could rise to 71 and the Cape Arago total to 49.

Both SPHON (1972) and BELCIK (1975) reported finding a *Pleurobranchus* sp. (Sphon from Strawberry Hill, and Belcik from Cape Arago). These specimens could be different from each other and *Berthella californica*, or one (or both) could be *B. californica*.

The *Trinchesia* sp. (which I have listed as *Cuthona* sp.) reported by BELCIK (1975) on *Tubularia* sp. in the Charleston boat basin could well be *Catriona columbiana*. In my experience in the area, only *Catriona columbiana*, *Flabellina trilineata*, and *Hermisenda crassicornis* occur on *Tubularia marina* (and *Cumanotus beaumonti* on *Tubularia crocea*—see below).

Until the *Eubbranchus* sp. collected by SPHON (1972) can be re-examined, it is impossible to ascertain whether it is an already described *Eubbranchus* species (including one of the two in Table 3) or belongs to an undescribed species.

SOWELL's (1949) report of *Cadlina pacifica* from Cape Arago is questionable. To my knowledge no other specimens of this dorid have been found since BERGH's (1879) description of three specimens collected by Dall in Alaska. Sowell reported finding at least five specimens and does not describe any aspect of them except (p. 22) that they were "always white about the same as the ground color of *Cadlina marginata*." My guess is that these were specimens of *Archidoris odhneri*, a white dorid that was undescribed at the time.

BELCIK (1965) found *Tritonia festiva* and *T. diomedea* (= *T. exsulans*), the two species of *Tritonia* presently known from the Pacific Northwest. It thus seems likely that the "whitish" *Tritonia* sp. he reported dredged off Cape Arago (BELCIK, 1965, 1975) is an undescribed species, possibly that pictured by BEHRENS (1980:103). For this reason I have not listed *Tritonia* sp. under the "questionable species" in Table 3.

BELCIK's (1965) Master's Thesis on the parasitic copepod *Ismaila monstrosa* Bergh contains an appendix listing 32 species of Oregon opisthobranchs that he had examined for parasites. Fifteen of these species were not found by SPHON (1972) and became the basis of BELCIK's 1975 paper. However, BELCIK (1975) includes an additional two species (*Trinchesia* sp., which I have listed as *Cuthona* sp., and *Archidoris odhneri*) that were not mentioned in his Master's Thesis. In addition, the appendix to his Thesis contains one species (*Fiona pinnata*) that Sphon did not find but that Belcik, for some reason, did not include in his 1975 paper. An "*Eolis* sp." is also mentioned in the Thesis and not in the 1975 paper. Presumably this is the same as the *Trinchesia* sp. mentioned above, and thus I have not included it in Table 3. I have included BELCIK (1965) as a reference in Table 3 in order to present the 17 additional species he found but did not include in this 1975 paper. Both BEHRENS (1980) and McDONALD & NYBAKKEN (1980) list Dillon Beach, Marin County, California as the northern limit of *Dirona picta*. However, BELCIK (1975) found it on the docks of the Charleston boat basin. I saw one specimen of *D. picta* collected by the summer 1983 O.I.M.B. invertebrate zoology class. The exact collection location is unknown.

SOWELL (1949) reported finding a form of *Hermisenda crassicornis* at North Cove "among *Laminaria* and *Costaria* and in association with *Triopha carpenteri* and *Dirona albolineata*." He further states "this form appears to be specifically distinct from *H. crassicornis*, but has not been definitely determined." This form is undoubtedly *Janolus fuscus*, which occurs in large numbers in the same habitat as *Triopha catalinae* and *Dirona albolineata*. BELCIK (1975) wrote that Sowell "confused this form with *Coryphella* sp. or *Antiopella* spp."

STEINBERG (1963b) recorded Coos Bay, Oregon, as the

Table 3
Benthic opisthobranchs known from Oregon.

Species	Reference*	Occurs at Cape Arago
<i>Acanthodoris hudsoni</i> MacFarland, 1905	2	
<i>Acanthodoris nanaimoensis</i> O'Donoghue, 1921	2, 5, 6, 8	x
<i>Adalaria</i> sp.	8	x
<i>Aeolidia papillosa</i> (Linnaeus, 1761)	1, 4, 5, 8	x
<i>Alderia modesta</i> (Loven, 1844)	4, 5, 8	
<i>Aldisa sanguinea</i> (Cooper, 1863)	1, 8	x
<i>Aldisa cooperi</i> Robilliard & Baba, 1972	8	x
<i>Ancula pacifica</i> MacFarland, 1905	8	x
<i>Anisodoris lentiginosa</i> Millen, 1982	8	x
<i>Anisodoris nobilis</i> (MacFarland, 1905)	1, 4, 5, 8	x
<i>Aplysiopsis smithi</i> (Marcus, 1961)	4, 5, 8	x
<i>Archidoris montereyensis</i> (Cooper, 1863)	1, 2, 5, 8	x
<i>Archidoris odhneri</i> (MacFarland, 1966)	4, 8	x
<i>Armina californica</i> (Cooper, 1863)	3, 5	
<i>Bathydoris</i> sp.	4, 5	
<i>Berthella californica</i> (Dall, 1900)	8	x
<i>Cadlina flavomaculata</i> MacFarland, 1905	1	
<i>Cadlina luteomarginata</i> MacFarland, 1966	1, 4, 5, 8	x
<i>Cadlina modesta</i> MacFarland, 1966	8	x
<i>Catriona columbiana</i> (O'Donoghue, 1922)	2, 8	x
<i>Crimora coneja</i> Marcus, 1961	8	x
<i>Cumanotus beaumonti</i> (Eliot, 1906)	8	
<i>Cuthona abronia</i> (MacFarland, 1966)	2, 8	x
<i>Cuthona albocrusta</i> (MacFarland, 1966)	2, 8	x
<i>Cuthona cocoachroma</i> Williams & Gosliner, 1979	8	x
<i>Cuthona flavovulta</i> (MacFarland, 1966)	8	x
<i>Cuthona fulgens</i> (MacFarland, 1966)	8	x
<i>Dendronotus frondosus</i> (Ascanius, 1774)	1, 2, 5, 8	x
<i>Dendronotus subramosus</i> MacFarland, 1966	8	x
<i>Diaphana californica</i> Dall, 1919	8	x
<i>Diaulula sandiegensis</i> (Cooper, 1863)	1, 2, 5, 8	x
<i>Dirona albolineata</i> Cockerell & Eliot, 1905	1, 2, 5, 8	x
<i>Dirona picta</i> MacFarland in Cockerell & Eliot, 1905	4, 5, 8	
<i>Discodoris heathi</i> MacFarland, 1905	1, 4, 5, 8	x
<i>Doto amyra</i> Marcus, 1961	8	x
<i>Doto columbiana</i> O'Donoghue, 1921	4, 5	x
<i>Doto kya</i> Marcus, 1961	8	x
<i>Elysia hedgpethi</i> (Marcus, 1961)	8	
<i>Eubbranchus olivaceus</i> (O'Donoghue, 1922)	8	x
<i>Eubbranchus rustyus</i> (Marcus, 1961)	8	x
<i>Fiona pinnata</i> (Eschscholtz, 1831)	5, 8	
<i>Flabellina fusca</i> O'Donoghue, 1921	2	
<i>Flabellina trilineata</i> (O'Donoghue, 1921)	2, 5, 8	x
<i>Hallaxa chani</i> Gosliner & Williams, 1975	8	x
<i>Hermæa vancouverensis</i> O'Donoghue, 1924	1, 8	x
<i>Hermisenda crassicornis</i> (Eschscholtz, 1831)	1, 2, 5, 8	x
<i>Hopkinsia rosacea</i> MacFarland, 1905	7	
<i>Janolus fuscus</i> O'Donoghue, 1924	1, 2, 4, 5, 8	x
<i>Laila cockerelli</i> MacFarland, 1905	1, 2, 5, 8	x
<i>Melanochlamys (Aglaja) diomedea</i> (Bergh, 1894)	3, 5	
<i>Melibe leonina</i> (Gould, 1852)	3	
<i>Onchidoris bilamellata</i> (Linnaeus, 1767)	1, 4, 5, 8	
<i>Onchidoris muricata</i> (Müller, 1776)	8	x
<i>Onchidoris</i> sp. (<i>O. hystricina</i>)	8	x
<i>Phyllaplysia taylori</i> Dall, 1900	3, 5	
<i>Placida dendritica</i> (Alder & Hancock, 1843)	8	x
<i>Polycera atra</i> MacFarland, 1905	8	x
<i>Polycera zosterae</i> O'Donoghue, 1924	8	
<i>Precuthona divae</i> Marcus, 1961	8	x
<i>Rostanga pulchra</i> MacFarland, 1905	1, 2, 5, 8	x

Table 3 (Continued)

Species	Reference*	Occurs at Cape Arago
<i>Tochuina tetraquetra</i> (Pallas, 1788)	4, 5	
<i>Triopha catalinae</i> (Cooper, 1863)	1, 2, 5, 8	x
<i>Triopha maculata</i> MacFarland, 1905	8	x
<i>Tritonia diomedea</i> Bergh, 1894	3, 5	x
<i>Tritonia festiva</i> (Stearns, 1873)	1, 2, 5, 8	x
<i>Tritonia</i> sp.	4, 5	
Questionable species		
<i>Cadlina pacifica</i> Bergh, 1879	1	x
<i>Cuthona</i> (<i>Trinchesia</i>) sp.	4	
<i>Eubranchius</i> sp.	2	
<i>Pleurobranchus</i> sp.	2	
<i>Pleurobranchus</i> sp.	4, 5	x

* 1, SOWELL (1949); 2, SPHON (1972); 3, references cited by SPHON (1972); 4, BELCIK (1975); 5, BELCIK (1965); 6, STEINBERG (1963a); 7, STEINBERG (1963b); 8, present study.

northern limit of *Hopkinsia rosacea*. This is the only record of *H. rosacea* north of Abalone Beach, Humboldt County, California (where a single specimen was found—see JAECKLE, 1984). Specimens of *H. rosacea* from Coos Bay were apparently collected by Lawrence Andrews, whom STEINBERG (1963a) cited as her source of opisthobranch specimens from Coos Bay. The only other species STEINBERG (1963a, b) reported from Coos Bay was *Acanthodoris nanaimoensis*.

BELCIK (1975) reported *Alderia modesta* as uncommon on *Vaucheria* mats on mudflats in Coos Bay. At least during the summer, *A. modesta* can be found in abundance feeding on mats of *Vaucheria* sp. in the South Slough of Coos Bay (personal observation).

Five additional species that I have observed in the Coos Bay area, but not at Cape Arago, are *Cumanotus beaumonti*, *Elysia hedgpethi*, *Fiona pinnata*, *Onchidoris bilamellata*, and *Polycera zosterae*. *Cumanotus beaumonti* occurs on *Tubularia crocea* (Agassiz, 1862) in the Charleston boat basin; a single specimen of *E. hedgpethi* was collected in Coos Bay by the summer 1983 O.I.M.B. invertebrate zoology class; *F. pinnata* occurs offshore on floating objects covered with its prey, the gooseneck barnacle *Lepas* sp.; *O. bilamellata* is found among *Balanus glandula* Darwin, 1854, on the pilings and breakwater of the Charleston boat basin; and a single *P. zosterae* was collected from a piling in the Charleston boat basin.

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Comparison of *Acteocina canaliculata* (Say, 1826), *A. candei* (d'Orbigny, 1841), and *A. atrata* spec. nov. (Gastropoda: Cephalaspidea)

by

PAUL S. MIKKELSEN AND PAULA M. MIKKELSEN

Harbor Branch Foundation, Inc., R.R. 1, Box 196,
Ft. Pierce, Florida 33450

Abstract. The type species of the genus *Acteocina*, *Acteon wetherilli* Lea, 1833, is synonymized with *Volvaria canaliculata* Say, 1826, type species of the genus *Utriculastra*; because *Utriculastra* and *Cylichnella* are synonymous, *Acteocina* is the senior synonym. The systematics of *A. canaliculata* and *A. atrata* spec. nov. are examined, and a neotype is designated for *A. canaliculata*. Descriptions are presented of shell, radular, and gizzard plate morphologies; geographic and bathymetric distributions are re-evaluated based on museum collections. Floridian specimens of *A. canaliculata* have planktotrophic development, hatching in 4 days and settling in 24 days; *A. atrata* has capsular metamorphic development, hatching in 9 days as benthic juveniles. A preliminary review of *Acteocina candei* (d'Orbigny, 1841) is given, and a lectotype is designated. *Acteocina candei* distinctly differs conchologically from *A. canaliculata*, is resurrected from synonymy, and is considered a valid species.

INTRODUCTION

Acteocina canaliculata (Say, 1826) and *A. candei* (d'Orbigny, 1841) are small, cephalaspid gastropods common throughout much of the western Atlantic. Intraspecific variability of shell and radular characters has obscured interspecific differences, making them consistently difficult to distinguish. Publications reporting either species may actually have considered both species simultaneously or confused the two.

Acteocina canaliculata and *A. candei* have been assigned to many genera, most notably *Utriculus* Brown, 1844, *Tornatina* A. Adams, 1850, *Retusa* Brown, 1827, and *Acteocina* Gray, 1847. *Acteocina* has had the most frequent usage in recent years. However, MARCUS (1956:41), MARCUS (1977:2), and CERNOHORSKY (1978:83) advocated restriction of the genus *Acteocina* to fossil forms because (1) the type species, *A. wetherilli* (Lea, 1833), was described as a fossil whose internal anatomy will never be known, and (2) knowledge of internal anatomy is necessary to define cephalaspid genera according to modern standards. Thus, they concluded that fossil species of this group cannot be reliably allocated to Recent genera. Following this reasoning, MARCUS (1977) allocated *A. canaliculata* and *A. candei* (which she synonymized with *A. canaliculata*) to *Utriculastra* Thiele, 1925. RUDMAN (1978)

incorrectly placed *A. canaliculata* (and thus *A. candei*) in the genus *Tornatina*, apparently unaware of MARCUS' (1977) work restricting *Tornatina* on the basis of radular and gizzard plate morphologies, and because he incorrectly believed that the genus *Cylichnella* Gabb, 1873, lacked jaws (see MARCUS, 1956:39; GOSLINER, 1979:88). GOSLINER (1979) determined that *Utriculastra* was a junior synonym of *Cylichnella* based on similar arrangements of the reproductive system. Therefore, according to the more recent literature, *A. canaliculata* and *A. candei* should be placed in the genus *Cylichnella*.

The familial placement of *Acteocina* (as *Cylichnella*, etc.) has likewise been varied; it has most recently been placed (MARCUS, 1977; RUDMAN, 1978; GOSLINER, 1980) in the Scaphandridae G. O. Sars, 1878. This family was considered (ABBOTT, 1974; CERNOHORSKY, 1978), apparently on a conchological basis alone, to be a junior synonym of Cylichnidae H. & A. Adams, 1854 (not of A. Adams, 1850, as stated by ABBOTT, 1974; not of Rudman, 1978). Although RUDMAN (1978:105) incorrectly repropounded Cylichnidae as a new family, he restricted the family to the genus *Cylichna* on the basis of anatomy. Therefore, according to Rudman, Cylichnidae and Scaphandridae are both valid and distinct families. GOSLINER (1980) refuted RUDMAN's (1978) distinction between Cylichnidae and

Scaphandridae, considering them synonymous. However, Gosliner chose Scaphandridae as the senior synonym, because he incorrectly considered Cylichnidae of Rudman, 1978, rather than of H. & A. Adams, 1854. Cylichnidae H. & A. Adams, 1854, is the proper senior synonym and would be the correct family for *Acteocina* following GOSLINER's (1980) synonymy. Following RUDMAN (1978), Scaphandridae is correct. The family Acteocinidae Pilsbry, 1921, may be valid as well (see CERNOHORSKY, 1978).

In 1962, WELLS & WELLS attempted to distinguish "*Retusa*" *canaliculata* from *Acteocina candei*. The diagnostic characters used were: radular characters (shape and number of denticles for lateral and rachidian teeth), protoconch appearance (degree of protrusion and number of whorls), shell shape (spire height, basal shape, convexity of the whorls, and apertural shape), habitat, and type of larval development. Wells & Wells found direct-developing larvae in field-collected egg masses of "*R.*" *canaliculata*, and assumed planktonic development in *A. candei* from the appearance of the protoconchs of the adults. However, FRANZ (1971a, b) found planktotrophic development in eggs deposited in the laboratory by adults of *A. canaliculata* collected from Connecticut. Franz explained this discrepancy by suggesting (1) that Wells & Wells, using field-collected egg masses from North Carolina, had unknowingly reared some other cephalaspid, (2) that poecilogony (multiple patterns of development within a species) exists for *A. canaliculata*, or (3) that cryptic species were present. GOSLINER's (1979) observations from the estuarine Pictou Harbor, Nova Scotia, also determined planktotrophic development for *A. canaliculata*.

MARCUS (1977:14) examined additional specimens of "*Utriculastra*" *candei* and "*U.*" *canaliculata* and determined that their shell and radular characters were highly variable and overlapping. Although Marcus noted different morphologies in the gizzard plates of each species, these differences were attributed to varying degrees of desiccation, and the plates were considered "identical." Possibly due to WELLS & WELLS' (1962) questionable developmental observations, MARCUS (1977) failed to address Wells & Wells' criterion of developmental type as a distinguishing character between the two species. Based on her observations, and on identical morphologies of the male reproductive structures, Marcus synonymized "*U.*" *candei* with "*U.*" *canaliculata*. This synonymy had been suggested many years earlier by DALL (1889:45).

Fifteen shells and 5 radulae of "*Utriculastra*" *canaliculata* were figured by MARCUS (1977), but no attempt was made to document further the degree of variability. MIKKELSEN & MIKKELSEN (1982) closely examined the shell and radular variability of "*U.*" *canaliculata* (as defined by MARCUS, 1977) and indicated that "*U.*" *candei* is an immature form of "*U.*" *canaliculata*, thus supporting the synonymy of Marcus. MIKKELSEN & MIKKELSEN (1983) noted the presence of two types of larval development in the "single species," "*Cylichnella*" *canaliculata*, and suggested that "*C.*" *candei* be resurrected as valid.

In the present study, embryonic, larval, and postlarval morphological characters, and examination of museum collections are utilized to:

- (1) show that Wells & Wells' "*Retusa canaliculata*" is actually an undescribed species, living sympatrically with *Acteocina canaliculata* in eastern Florida;
- (2) determine the correct generic placement for *A. canaliculata* and *A. candei*;
- (3) examine in detail the postlarval intraspecific variation of the shell, radula, and gizzard plates of *A. canaliculata* and the new species;
- (4) describe the larval development of *A. canaliculata* as well as that of the new species; and
- (5) partially characterize *Acteocina candei*, in contrast with *A. canaliculata* and the new species.

MATERIALS AND METHODS

Collections

The principal study site was the 195 km-long Indian River lagoon, along the central east coast of Florida (Figure 7D). Salinity generally ranged from 18 to 36 ppt, although extremes of 8 and 42 ppt were recorded during the study. Live snails were sieved, using 0.5 mm-mesh screens, from bare or vegetated subtidal sand or mud substrates. Dried or wet-preserved specimens from various museums and private collections were utilized to redetermine geographic and bathymetric distributions. Fossil type specimens were examined for synonymies; however, because additional fossil material was not thoroughly studied, detailed paleontological distributions are not given. Cited repositories and other sources are as follows:

- ANSP—Academy of Natural Sciences of Philadelphia, Philadelphia, PA
- BM(NH)—British Museum (Natural History), London
- CAS—California Academy of Sciences, San Francisco, CA
- ChM—Charleston Museum, Charleston, SC
- D. Franz Collection—Department of Biology, Brooklyn College of the City University of New York, Brooklyn, NY
- HMNS—Houston Museum of Natural Science, Houston, TX
- IRCZM—Indian River Coastal Zone Museum, Harbor Branch Foundation, Ft. Pierce, FL
- MACN—Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
- MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, MA
- MORG—Museo Oceanográfico, Rio Grande, Brazil
- PRI—Paleontological Research Institution, Ithaca, NY
- ROM1Z—Royal Ontario Museum, Toronto, Ontario, Canada
- R. Van Dolah Collection—South Carolina Marine Resources Research Institute, Charleston, SC
- UNC-IMS—Institute of Marine Sciences, University of North Carolina, Morehead City, NC

USNM—National Museum of Natural History, Washington, DC.

In synonymies, a dagger (†) preceding a species name indicates fossil type specimens. In "Material examined" sections, an "L" indicates that at least some of the specimens in the lot were live-collected and contained soft parts; an "E" indicates that all specimens were empty shells.

Either original figures or type specimens were examined of all western Atlantic *Acteocina canaliculata*-like forms, fossil and Recent, described to date. Types were examined if figures even remotely resembled the species discussed herein. Two exceptions were *Cylichna virginica* Conrad, 1868, and *Tornatina cylindrica* Emmons, 1858, for which no types could be located to clarify the ambiguous original figures.

Postlarval Observations

Specimens with intact protoconchs, collected from various localities throughout the study area, were chosen for statistical analyses. These encompassed a wide range of shell lengths, but excluded specimens not retained by the 0.5 mm-mesh collecting sieve. Each shell was illustrated using a stereomicroscope and camera lucida providing permanent records of shell length, shell width, spire height and angle (Figure 1A), and percent of protoconch protrusion (Figure 1D). Drawings were essential because partial destruction of the shells was necessary to remove the retracted animals.

Percent of protoconch protrusion was determined (Figures 1E–G) utilizing the circle, $(x - h)^2 + (y - k)^2 = r^2$, approximated by the periphery of the protoconch, where (h, k) are the coordinates of the center, (x, y) are the coordinates of any point on the circle, and r is the radius. With the ordinate axis drawn through the center of the circle, and the abscissa through the lateral suture points of the protoconch with the first postnuclear whorl, the y-coordinate (h) of the center equals zero, and the equation reduces to Equation I: $x^2 + (y - k)^2 = r^2$. Measurement of the protoconch's exposed height (b) and width at the suture $(2a)$ yields 3 points on the circle: $(a, 0)$, $(-a, 0)$, and $(0, b)$. For point $(a, 0)$ or $(-a, 0)$, $y = 0$, and Equation I becomes Equation II: $a^2 + k^2 = r^2$. For point $(0, b)$, $x = 0$, and Equation I becomes Equation III: $b^2 - k^2 = r^2$ or Equation IV: $b - k = r$. Subtracting Equation II from Equation III yields Equation V: $k = (b^2 - a^2)/2b$. Using a and b obtained from actual protoconch measurements, Equation V can be solved for k , which is used in Equation IV to determine the radius: $r = b - (b - a)/2b$. The diameter of the circle $(2r)$ and the exposed height (b) are then used to determine the percentage (P) of protoconch protrusion: $P = b/2r \times 100\%$.

Radulae and gizzard plates were extracted by dissolving the surrounding soft tissue in a solution of 10% sodium hydroxide at 20°C (LINDBERG, 1977). In addition to suggestions by TURNER (1960) and SOLEM (1972), handling

of small radulae was facilitated by use of a cat's vibrissa mounted on the tip of a probe. Gizzard plates were observed and subsequently stored in 70% ethanol, or dried. Radulae were simultaneously stained and permanently mounted on glass slides, using Turtox CMC-9AF low-viscosity stain-mountant tinted with acid fuchsin (Masters Chemical Co., Inc., Des Plaines, IL). Due to the extremely small size of the radula, this one-step operation eliminated the loss of many radulae. Each radula was mounted so that at least some of the lateral teeth were oriented as in Figure 1B. All slide-mounted radulae were illustrated using a compound microscope and camera lucida. These drawings provided the width, angle, and number of denticles for lateral teeth (Figure 1B), plus the width and number of denticles for rachidian teeth (Figure 1C). Radulae used for scanning electron microscopy were cleaned by sonication, following the method of SOLEM (1972). Radulae and gizzard plates were air dried and scanned using a Zeiss Novascan-30.

Shell terminology is after SMITH (1967a:758–760) and KNIGHT (1952:7–9); radular terminology is after BERTSCH (1977). Providing regressions of various characters follows the initiative of BERTSCH (1976).

Larval Development

Adults were collected during each month of the year from at least one of several locations (Figure 7D). Adults from a single site were left together for about 24 h in a finger bowl with seawater and sand substrate from the collection site. Individuals were then isolated in compartmented plastic trays, each containing filtered seawater and a thin layer of sand. Each compartment was checked daily, for up to 14 days, and egg masses were removed to compartmented plastic trays containing seawater only. Adults and developing egg masses were maintained at ambient laboratory conditions of 22–25°C with variable lighting, or under incubation at 22°C with a daily light cycle of 12 h light/12 h dark.

Planktotrophic larvae were reared using larval culture sieves placed in 300-mL beakers. Each larval sieve consisted of a 4.5-cm section of acrylic tubing, 7.6 cm in diameter, closed at the base by a 33 μm -mesh nitex screen. Larvae from a single egg mass were reared in the same sieve. Survivorship was maximized by adding antibiotics (5 mg/mL streptomycin sulfate plus 5 mg/mL penicillin-G) to 0.5 μm -filtered, 36-ppt seawater (SWITZER-DUNLAP & HADFIELD, 1981:207). Cetyl alcohol flakes were floated on the water to prevent larvae from being trapped by the surface tension (HURST, 1967). Veligers were fed to excess with *Stephanoptera* sp., a 10 μm -diameter, unicellular green alga. Water and food supply were changed every other day.

Direct-developed hatchlings and metamorphosed planktic larvae were transferred to 300-mL beakers of filtered seawater. Amorphous organic material, collected

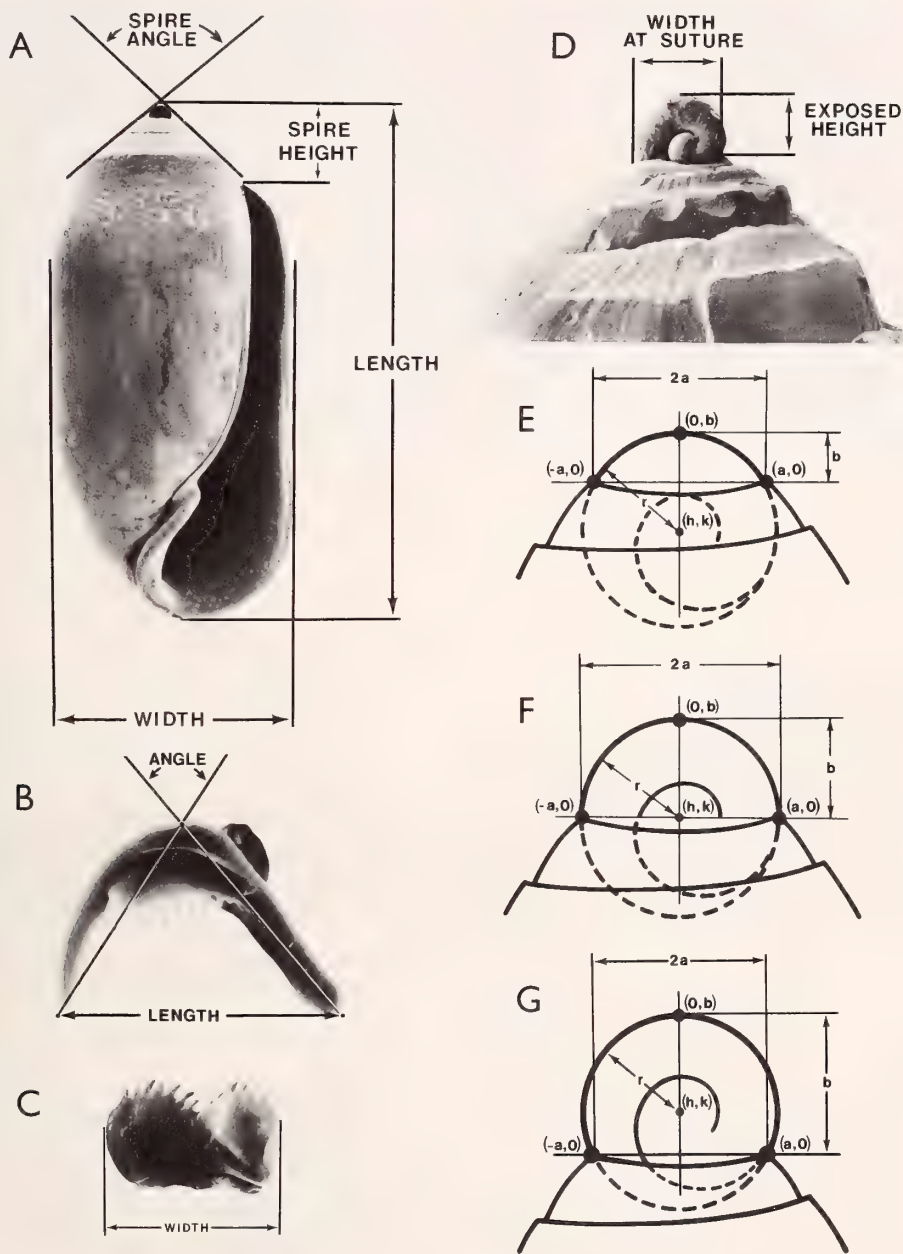


Figure 1

Shell and radular parameters. A. Shell in apertural view. B. Lateral radular tooth. C. Rachidian radular tooth. D. Apical view of protoconch. E, F, and G. Diagrammatic protoconchs of increasing degree of protrusion, showing points and distances used in calculating percent protrusion.

from sedimentary detritus at the collection site or from a laboratory running-seawater system, provided food for the juveniles. After this material was suspended by swirling, the larger particles were allowed to settle and the finer suspended material was decanted off. It was this fine organic material which was added in small quantities to the

beakers containing the juveniles, to form a thin bottom layer of food. Juveniles were visually located and transferred to new seawater and food once a week.

Larval shells were prepared for SEM either by preservation in 80% ethanol or by soaking in a dilute solution of household bleach to remove the soft tissues. The latter

method was considered least desirable because opercula were invariably lost. The larval shells were then dried, mounted, and scanned as described above for the radulae and gizzard plates.

SYSTEMATIC RESULTS

Genus *Acteocina* Gray, 1847

Acteocina GRAY, 1847:160.

Cylichnella GABB, 1873:273–274.

Utriculastra THIELE, 1925:235.

The holotype of *Acteon wetherilli* Lea, 1833 (type species of the genus *Acteocina*) is extremely worn, and lacks its protoconch. The type locality of *A. wetherilli* is Deal, New Jersey, from deposits of Miocene age (RICHARDS, 1968). L. D. Campbell (personal communication, 1983) indicated that the type locality may be as young as Pleistocene.

In all discernible conchological characters, *Acteocina wetherilli* agrees with the Recent species *Volvaria canaliculata* Say, 1826, type species of the genus *Utriculastra*. This synonymy was first suggested by OLSSON & HARBISON (1953) and reiterated by OLSSON & MCGINTY (1958), OLSSON (1964), and CAMPBELL *et al.* (1975). The genus *Acteocina* is therefore applicable to Recent forms (contrary to MARCUS, 1956:41). The anatomical characteristics of *A. canaliculata* may now be assumed to be applicable to the genus. In addition, the genus *Utriculastra* becomes a junior synonym of *Acteocina*.

Utriculastra and *Cylichnella* are presently synonymous, in accordance with the anatomical studies of GOSLINER (1979). Although GOSLINER (1979) additionally included *Tornastra* Marcus, 1977, in this synonymy, we prefer to omit it here because of the distinctive gizzard plate and radular anatomy of *Bulla eximia* Baird, 1863, the type species of *Tornastra* (see MARCUS, 1977). DALL (1908) listed eight additional synonyms of *Cylichnella*, but they are either incorrect or unconfirmed herein.

Our experience has determined that *Acteocina*-like species can be distinguished conchologically. In the case of *Acteocina*, we have conchologically matched its fossil type specimen with a Recent species, and have subsequently defined the genus using the internal characteristics of Recent specimens. This action does not differ from the conchological matching of dead-collected Recent type specimens (of prosobranch and other mollusks) with living individuals, which are then used to redescribe the species, complete with internal anatomy. Although this procedure is followed frequently in malacology, it has been considered inappropriate for cephalaspids (MARCUS, 1956;

MARCUS, 1977). In our opinion, it must be considered acceptable (for example, in the case of *A. candei*).

Until further studies at the species level are complete for *Acteocina* and other closely related genera, resolution of the familial placement of *Acteocina* is not possible.

Acteocina canaliculata (Say, 1826)

(Figures 2 to 5)

Volvaria canaliculata SAY, 1826:211.

[non *Bulla canaliculata* D'Orbigny, 1841:133–134; 1842: pl. 4 bis, figs. 21–24.]

Bullina canaliculata: SAY, 1832:pl. 39.

†*Acteon wetherilli* LEA, 1833:213, pl. 6, fig. 224.

Bulla obstricta GOULD, 1840:196.

†*Acteocina chowanensis* RICHARDS, 1947:34, pl. 11, fig. 10.

Acteocina canaliculata: FRANZ, 1971a:68–69; 1971b:174–182.

Utriculastra canaliculata: MARCUS, 1977:14–17 (in part), figs. 36–38, 40, 42.

Utriculastra canaliculata: MIKKELSEN & MIKKELSEN, 1982: 38.

Cylichnella candei: MIKKELSEN & MIKKELSEN, 1983:91.

Material examined

Neotype (designated herein): 3.80 mm, ANSP A9721A.

Specimens collected with the neotype: 11L, ANSP A9721B; 9L, IRCZM 65:1910; 2L, IRCZM 65:1911; radula slide, IRCZM 65:M055; 11L, USNM 836099; 10L, ChM IN 19869; 10L, MCZ 272599.

Type material of synonyms:

†*Acteon wetherilli* Lea, 1833: holotype, ANSP 14431. Miocene (?Pleistocene), New Jersey.

Bulla obstricta Gould, 1840: 14 syntypes (+4 shell fragments), MCZ 216773. New Bedford, Massachusetts.

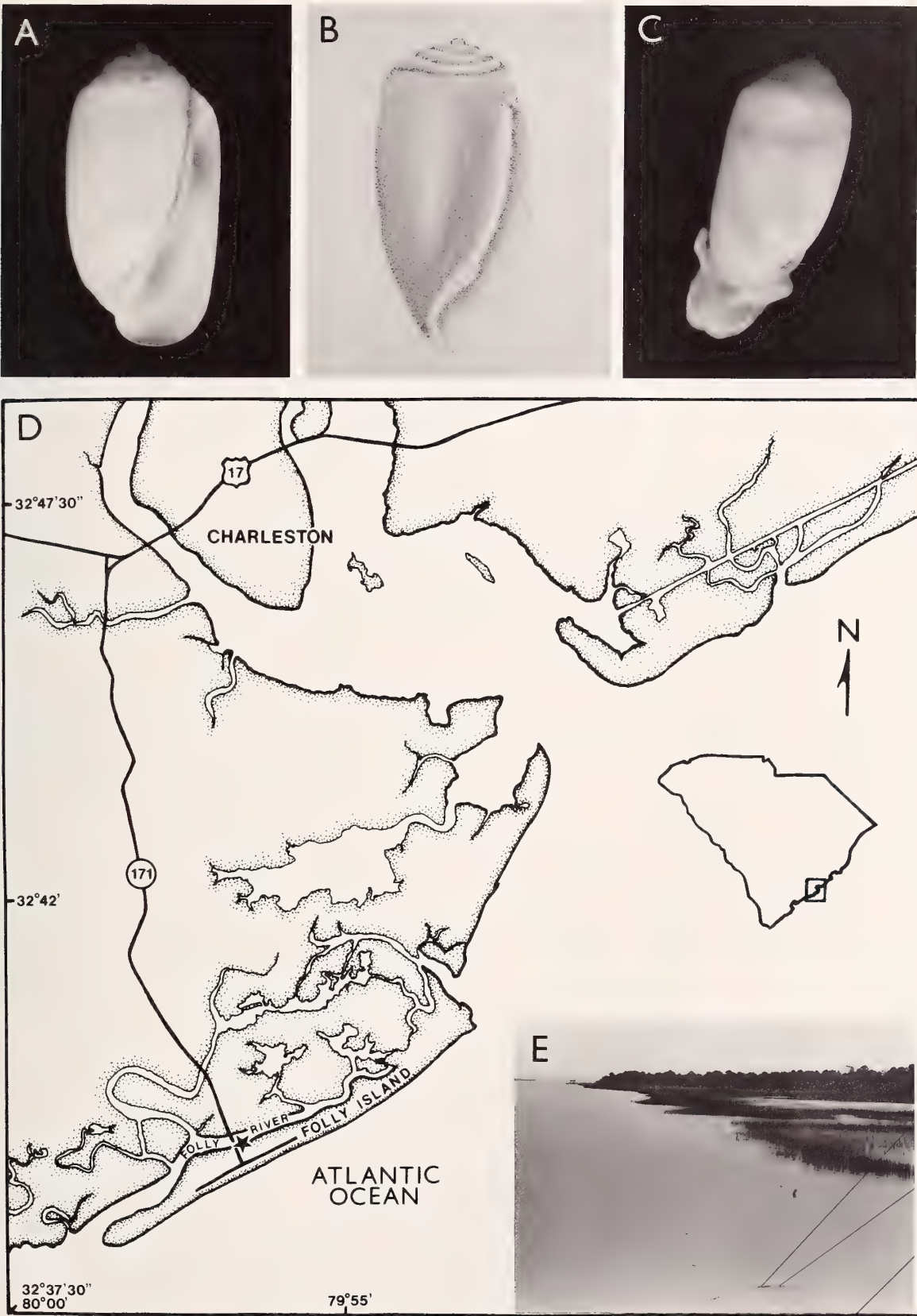
†*Acteocina chowanensis* Richards, 1947: holotype, ANSP 16754. Yorktown Formation, Miocene, North Carolina.

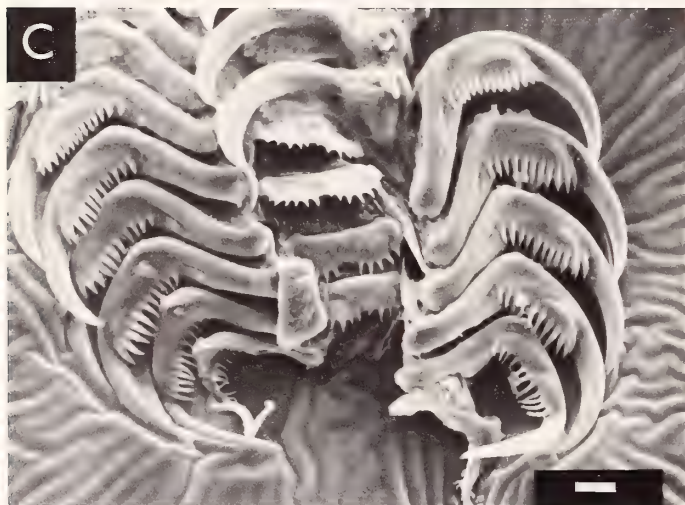
Other material: *Prince Edward Island*: 34L, MCZ 38870.—

Maine: Isle au Haut(?): 10E, MCZ ex.14531 (in part).—*Massachusetts*: Duxbury: 76L, USNM 358256.—New Bedford: 24L, USNM 57310.—*Rhode Island*: Westerly: 200+L, USNM 358281.—*Connecticut*: Noank (Beebe Cove), 20L, D. Franz Collection.—*New Jersey*: Little Egg Harbor: 8E, D. Franz Collection.—*Maryland*: Point No Point: 100+L, USNM 379507.—*North Carolina*: Cape Hatteras: 3L, D. Franz Collection.—off Cape Lookout: 500+L, USNM 523583.—*Neuse River*: 51L, UNC-IMS 9859.1–.51.—*South Carolina*: Charleston Harbor: 3E, ChM 30.183.11.—*Georgia*: Jekyll Island: 12E, UNC-IMS 8074.1–12.—*Florida*: St. Augustine: 18E, USNM 358292 (in part).—Cape Canaveral: 4E, ChM 43.28.4734.—Merritt Island (Pleistocene fossils): 6E, IRCZM 65:2000.—Turnbull Creek (vouchers): 14L,

Figure 2

Acteocina canaliculata. A. Neotype, 3.80 mm, ANSP A9721A. B. SAY's (1832) original figure. C. Neotype, crawling animal. D. Map of Charleston, SC, area showing Folly River collection site for the neotype. E. Folly River site at high tide.





USNM 804403; 22L, IRCZM 65:1671.—Round Island (vouchers): 50L, ROM1Z B2462; 10L, ROM1Z B2464; 10L, USNM 804404; 10L, IRCZM 65:1672.—Lantana: 86E, ANSP 180523 (in part).—Miami: 224E, USNM 270719 (in part).—Rabbit Key, Monroe Co.: 4E, ANSP 105428.—Cape Romano: 8E, ANSP 92061.—Sanibel Island: 84L, MCZ 84334.—Charlotte Harbor: 68L, USNM 83763.—Clearwater Bay: 117L, ANSP 9446.—Cedar Keys: 39L, MCZ 242896.—St. Joseph Bay: 3L, ANSP 83771.—off Ft. Walton: 7L, MCZ 145871.—Louisiana: Timbalier Island: 27L, HMNS 9231.—Texas: Galveston: 27L, HMNS 8134.—Matagorda Bay: 64L, HMNS 9238.—Corpus Christi: 10E, USNM 125553.

Original description

Acteocina canaliculata was originally described from specimens taken from the coast of South Carolina. The type locality is believed to be in the vicinity of Charleston, where the collector, Mr. Stephen Elliott, lived (MAZYCK, 1913) and probably did the majority of his collecting. SAY (1826:211) briefly described the species: "Shell whitish, immaculate, cylindric, with very minute obsolete wrinkles; spire convex, very little elevated, mammillated at the tip; volutions above five, with their shoulder very obtusely grooved; labrum with the edge arcuated; labium overspread with a calcareous lamina, and with a single oblique fold or small tooth near the base." Say also stated that "the arcuated form of the edge of the labrum is only perceived when the part is viewed in profile." Although a figure did not accompany the original description, the species was figured later (as *Bullina canaliculata* in "American Conchology" (SAY, 1832:pl. 39) and is reproduced herein (Figure 2B).

Type material

A series of 25 specimens of *Acteocina canaliculata* labeled as syntypes was procured from the Academy of Natural Sciences of Philadelphia (ANSP 57312). However, these are probably not type specimens because: (1) the specimen label reads "*T. canaliculata*," indicating the genus *Tornatina*, (2) the cited locality is "Georgia," and (3) "J. S. Phillips" is recorded as donor of the lot. Thus, the status of ANSP 57312 as a type lot is questionable.

A search (by ANSP personnel) of the remaining lots of *Acteocina canaliculata* and related species in the ANSP collections failed to yield the original type material. Historical information obtained from Virginia O. Maes (personal communication, 1982) indicates that the types were probably destroyed. According to her, Say removed his

molluscan collections from the ANSP to New Harmony, Indiana in 1825 where much of his material was subsequently lost in a fire. Long after Say's death in 1884, his wife returned whatever was salvaged of Say's collections to Dr. H. A. Pilsbry at the ANSP. Unfortunately, no records exist of the species involved in these transactions, and we conclude that the types of *Volvaria canaliculata* were probably destroyed in the New Harmony fire. To the best of our knowledge, a neotype has not been designated.

Lacking any type specimens, one must rely entirely upon the original description by Say and his subsequent illustration. Unfortunately, the description and figures could apply to any of several species of *Acteocina*. However, a survey of South Carolina material in museum collections (USNM, ANSP, MCZ, ChM) and from Dr. L. Campbell (University of South Carolina at Spartanburg) included only one species living in shallow, estuarine waters (equivalent to SAY's [1826] "coast of South Carolina"). This species closely approximates Say's original illustration. In addition, the majority of specimens labeled as *A. canaliculata* in early museum collections were also of this same form. We take this as sufficient evidence to consider the species in South Carolina estuaries to be Say's *Volvaria canaliculata*.

Following the determination of Say's *Volvaria canaliculata*, designation of a neotype was necessary to avoid future confusion. On December 3, 1982, specimens of *Acteocina canaliculata* were collected by the authors from soft, subtidal mud, below zones of *Spartina* and oysters in the Folly River, an estuarine channel just south of Charleston Harbor, Charleston County, South Carolina (Figures 2D–E). The site was located adjacent to the State Route 171 bridge over the Folly River. Salinity ranged (on an incoming tide) from 27 to 30 ppt during collection of the specimens. The neotype and specimens collected with it were distributed to various repositories (see Material examined, above).

A redescription of *Acteocina canaliculata* follows, based primarily on our observations of Indian River specimens, but consistent with material from South Carolina.

Diagnosis

Teleoconch thick-walled, cylindrical to pyriform. Shoulder rounded; subsutural sculptural band indistinct. Spire height variable, but usually less than 20% of total shell length. Protoconch distinctly tapered toward its origin, showing strongly coiled sutures in lateral view. Lat-

Figure 3

Acteocina canaliculata, adults. A. Shell, from Indian River lagoon, in apertural view, 4.58 mm. B. Gizzard plates, view of grinding surfaces. C. Radula with lateral teeth reflected to expose rachidians. D. Lateral teeth, showing wing-like expansion with denticles. E, F, and G. Protoconch: E. "Apical" view. F. "Posterior" view. G. "Umbilical" view. Scales: B = 100 μ m; C = 10 μ m; D = 5 μ m; E, F, and G = 50 μ m.

eral radular teeth with wing-like expansion bearing one row of denticles. Unpaired gizzard plate T-shaped. Tissues of gizzard, pallial caecum, and Hancock's organs light orange to pink in live material.

Distribution

Prince Edward Island, Canada; Maine (dead shells only); Massachusetts to peninsular Florida and entire Gulf coast to Texas; intertidal to 40 m.

Description

Shell characters

The orthostrophic, dextral teleoconch of adult *Acteocina canaliculata* is smooth and cylindrical, and has up to three whorls (Figure 3A). Large specimens tend toward a pyriform shape, i.e., with greater shell width at the posterior end. The aperture is narrow posteriorly and flares anteriorly; it extends from 80 to 94% of the shell length. The parietal area bears a slight callus, ending in a columella with a single fold. The shell walls are porcelainous white and thick, approximately 175 μm at the midpoint of the body whorl of adults. The shoulder is somewhat keeled in young to immature individuals, becoming more rounded with maturity, with an indistinct, impressed, subsutural sculptural band. Indian River specimens attained a shell length and width of 5.0 mm and 2.3 mm respectively; the specimens varied in spire angle from 76 to 142 degrees and in spire height from 6 to 20%. The periostracum is thin and transparent, unless environmentally stained, in which case it is often spirally banded.

The sutures of the smooth, hyperstrophic, sinistral protoconch (Figures 3E, G) are strongly curved in both "lateral" views (i.e., from the larval shell's umbilical or apical aspect), appearing slightly umbilicate in "umbilical" view. In its "posterior" view (Figure 3F), the protoconch tapers toward its distal end, or origin. The percent of protoconch protrusion varied from 25 to 74%.

Correlation coefficients (r) were calculated for shell length versus the four other characters measured (Table 1). Shell length versus shell width showed the strongest r -value, while percent of protoconch protrusion, percent spire height, and spire angle yielded very low coefficients. Percent spire height versus spire angle showed a fairly strong negative coefficient.

Radular characters

The radular formula of *Acteocina canaliculata* is 1-R-1 (Figure 3C), with 11-19 rows in specimens 2 mm or more in length. The rachidian teeth ranged in width from 17 to 34 μm and are centrally notched, with each rounded half bearing 4-11 sharply pointed denticles. The lateral teeth (Figure 3D) are sickle-shaped and unicuspid, with the cusp bearing a wing-like expansion supporting one row of several denticles. A blunt, basal tubercle is present for articulation with adjoining lateral teeth. Ontogenetic

increases were noted in the lateral teeth in number of denticles from 6 to 18, in width from 41.6 to 71.9 μm , and in angle from 79 to 104 degrees. Variation in number of lateral tooth denticles within a single radula was also noted (Figure 3C). Shortly after metamorphosis, lateral teeth of juveniles were about 15 μm in length, and smooth; faint traces of denticles were evident on some lateral teeth at 7-9 days post-metamorphosis.

Correlation coefficients (r) for shell length versus radular characters (Table 1) were generally low, with the exception of lateral and rachidian tooth widths. Lateral tooth width versus lateral tooth angle ($r = 0.06$) and shell length versus lateral tooth angle ($r = 0.01$) were particularly low.

Other features

The extended, living animal of *Acteocina canaliculata* is of typical cephalaspid form (Figure 2C). The foot and mantle are translucent white in color, with scattered opaque white dots. Although the shell walls are thick and porcelainous, they are translucent enough to allow limited observation of the internal anatomy. The gizzard, pallial caecum, and Hancock's organs are light orange to pink in color.

The calcified portion of the gizzard of *Acteocina canaliculata* consists of three plates (Figure 3B): a "pair" of non-identical, but similarly elongated, plates opposing a larger "unpaired" plate. The unpaired plate is most dorsal in the crawling animal and is distinctly T-shaped, regardless of the method of extraction, preparation, or degree of desiccation.

The reproductive system did not differ in gross arrangement from that described by MARCUS (1977) or GOSLINER (1979).

Oviposition

Oviposition in the laboratory occurred at all hours except those between 1800 and 2400. Egg masses were usually deposited within the first few days after collection of the adults. Spawning occurred monthly in the field and in the laboratory, giving no indication of reproductive seasonality in the Indian River Lagoon animals.

Egg mass

The egg mass of *Acteocina canaliculata* (Figure 4A) corresponds to "type C" of HURST's (1967) opisthobranch egg mass forms. It is gelatinous and ovoid, ranging in maximum diameter from 1.9 to 6.4 mm (mean = 3.7 mm). It is firmly anchored at the sediment surface by a mucous thread, up to 60 mm long, which may bifurcate one or more times. Fresh egg masses were usually coated with sand grains, although most fell off within the first few hours after deposition. Uncleaved egg diameters ranged from 63.2 to 85.4 μm (mean = 77.5 μm). The number of eggs per mass ranged from 189 to 1293 (mean = 631 eggs/

Table 1

Statistical analysis of characteristics examined in *Acteocina canaliculata* and *A. atrata* spec. nov.; r , correlation coefficient; $y = mx + b$, regression line equation; n , number of cases; **, not applicable.

Character x	vs.	Character y	<i>Acteocina canaliculata</i>			<i>Acteocina atrata</i>		
			r	$y = mx + b$	n	r	$y = mx + b$	n
Shell length	vs.	Shell width	0.93	$y = 0.445x + 0.163$	56	0.98	$y = 0.490x + 0.0534$	49
Shell length	vs.	Percent spire height	0.09	$y = 0.358x + 13.6$	56	0.27	$y = 1.30x + 8.16$	49
Shell length	vs.	Spire angle	-0.23	$y = -4.05x + 114$	56	-0.57	$y = -11.6x + 153$	49
Shell length	vs.	Percent protoconch protrusion	0.10	$y = 1.31x + 52.1$	56	0.20	$y = 2.03x + 49.0$	49
Shell length	vs.	Radular rows	0.20	$y = 0.506x + 12.7$	56	0.52	$y = 0.975x + 12.2$	49
Shell length	vs.	Lateral tooth denicules	0.48	$y = 1.83x + 5.08$	56	0.18	$y = 0.638x + 17.2$	49
Shell length	vs.	Rachidian tooth denicules	0.46	$y = 0.775x + 3.82$	56	0.52	$y = 0.797x + 4.46$	49
Shell length	vs.	Lateral tooth width	0.85	$y = 8.79x + 25.5$	56	0.92	$y = 13.5x + 18.4$	49
Shell length	vs.	Rachidian tooth width	0.76	$y = 3.91x + 11.1$	56	0.79	$y = 3.83x + 15.5$	49
Shell length	vs.	Lateral tooth angle	0.01	$y = -0.07x + 92.6$	56	0.54	$y = 4.33x + 92.9$	49
Lateral tooth width	vs.	Lateral tooth angle	0.06	$y = 0.047x + 89.8$	56	0.60	$y = 0.326x + 86.6$	49
Lateral tooth width	vs.	Lateral tooth denicules	0.52	$y = 0.190x + 0.79$	56	0.60	$y = 0.0526x + 15.9$	49
Lateral tooth width	vs.	Rachidian tooth width	0.76	$y = 0.374x + 3.70$	56	0.82	$y = 0.270x + 11.2$	49
Rachidian tooth width	vs.	Rachidian tooth denicules	0.55	$y = 0.185x + 1.96$	56	0.58	$y = 0.181x + 2.02$	49
Percent spire height	vs.	Spire angle	-0.77	$y = -3.54x + 153$	56	-0.82	$y = -3.49x + 156$	49
Shell length	vs.	Number of eggs	0.90	$y = 393x - 801$	32	0.55	$y = 38.2x - 56.6$	54
Shell length	vs.	Egg mass diameter	0.88	$y = 1.42x - 1.46$	32	0.41	$y = 0.534x + 1.42$	54
Shell length	vs.	Egg tube diameter	**	**	**	0.42	$y = 92.3x + 256$	26
Shell length	vs.	Egg diameter	0.72	$y = 10.4x + 39.9$	7	0.22	$y = 5.19x + 131$	15
Shell length	vs.	Egg capsule length	-0.10	$y = -2.46x + 163$	15	0.02	$y = 0.91x + 317$	21
Shell length	vs.	Egg capsule width	-0.50	$y = -6.36x + 150$	15	-0.30	$y = -8.39x + 294$	21
Egg capsule length	vs.	Egg capsule width	0.56	$y = 0.302x + 83.7$	15	0.60	$y = 0.373x + 143$	21

mass). Each egg was encased in an oval capsule, about $155 \times 130 \mu\text{m}$ (range: $141\text{--}174 \times 121\text{--}139 \mu\text{m}$); capsules were interconnected by chalazal material. No internal transparent tubes, nurse eggs, or auxiliary yolk-like material were present. Statistical analyses showed high correlation coefficients (r) for maternal shell length versus egg diameter, egg mass diameter, and number of eggs per mass (Table 1).

Larval development

Acteocina canaliculata exhibits planktotrophic development. Pre-hatching development was rapid and consistent between egg masses. The first two cleavages, to 2 cells at 2.5 h and to 4 cells at 3.5 h, are total, spiral and equal, after which they are unequal and form distinct animal and vegetal poles. The 8-celled stage appears at 4.5 h followed by the 16-celled stage at 5 h into development. Further development proceeds rapidly to a multicelled or blastula stage, and by 23 h to a heart-shaped gastrula with its slit-like blastopore clearly visible.

The trochophore stage forms, and it begins to spin on its lateral axis (effectively doing "backwards somersaults") at about 28.5 h into development. The mouth, metapodial rudiment, and prototroch bearing fine cilia are clearly visible at this stage, and the vegetal pole appears as an undifferentiated spherical mass. Two anal cells appear on the lower right surface of the visceral hump.

The third day of development is characterized by the appearance of the rapidly spinning veliger stage (Figure 4B). By then, the larva has switched to an antero-posterior axis of rotation. A well-developed velum with long cilia, a subvelum, two otocysts, a paucispiral operculum beneath a pointed metapodium, a ciliated median metapodial band, and a spherical embryonic shell approximately $85 \mu\text{m}$ in diameter are present. As with other opisthobranchs, torsion does not occur as a larval process, except in the migrating anal cells, and the viscera differentiate in their post-torsional positions. On the 4th day of development, the veliger (Figure 4C) has a large, well-formed right eye. Its shell averages $140 \mu\text{m}$ long, and is nearly symmetrical, being only slightly skewed to the larval left. A colorless, larval kidney is prominent adjacent to the anus, and cilia are visible within the lumen of the midgut. Hatching can be mechanically stimulated by handling or rupturing the egg mass at about 90 h, but if not induced, will occur by 100–110 h after deposition. Hatching is rapid and nearly synchronous, being completed (*i.e.*, the entire mass emptied) within 10 to 20 min.

Post-hatching development depended greatly on the de-

gree of feeding by individual larvae. A large proportion (77.4%) of the hatched veligers in our most successful culture did not metamorphose; most of these were apparently unable to feed, as evidenced by their colorless digestive systems and little or no growth. The remaining individuals (22.6%) began feeding immediately, as evidenced by the bright green coloration of their guts, and developed rapidly. Acquisition of juvenile characteristics after hatching was a function of the degree of growth, expressed as shell length, rather than age of the specimen. The degree of development among the individuals in a culture was also highly variable.

When larvae were not fed, many individuals survived for two weeks although no shell growth was observed. Although the left eye appeared in some individuals after four days, it remained smaller than the first-formed right eye. The left digestive diverticulum noticeably decreased in size during this period. All starved larvae died by the third week after hatching.

In feeding individuals, the left eye appeared, and equaled the right in size, by the fourth post-hatching day at $163 \mu\text{m}$ shell length. By $270 \mu\text{m}$ shell length, the propodium began to swell, the right side of the mantle opened, and the larval heart began pulsating.

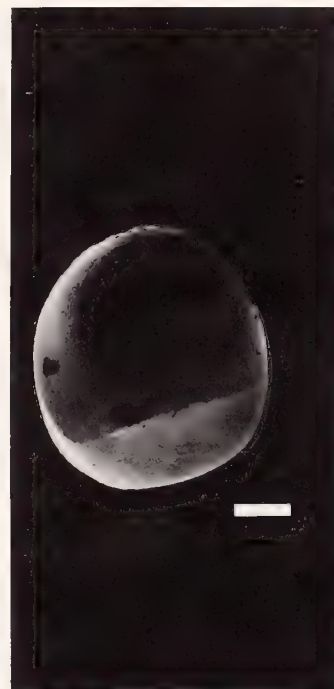
Metamorphosis at $300 \mu\text{m}$ shell length (Figures 5A–C) began after 14 to 20 days, independent of any special substrate. In newly metamorphosed individuals, both larval and adult hearts beat actively, and the nearly umbilicate aspect of the shell was visible from the larval right (Figure 5A). Immediately after metamorphosis, shell growth accelerated at the larval right, beginning the change in direction of coiling. Shells of juveniles approximately one week post-metamorphosis are shown in Figures 5D and E. Attempts at rearing *A. canaliculata* juveniles past this stage of development were unsuccessful.

Remarks

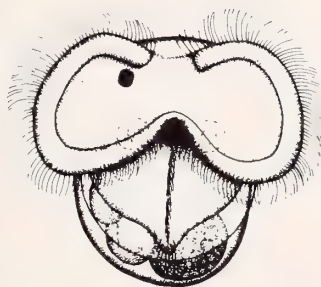
Specimens of *Acteocina canaliculata* show a strong resemblance to those of *Retusa obtusa* (Montagu, 1803), especially in New England where the two species overlap in distribution. Living or live-collected material of *R. obtusa* may be distinguished from *A. canaliculata* by the presence of a much thinner shell and by the absence of eyes and a radula. In the chalky condition often found in dead shells, however, the two species are more similar in appearance, and one must rely upon conchological characters alone. The bulbous protoconch of *R. obtusa*, indicating direct development, is the most reliable feature in these

Figure 4

Acteocina canaliculata, larval development. A. Egg mass. B and C. Larval stages showing appearance of larvae and corresponding larval shells. B. Early veliger in egg capsule, three days post-deposition. C. One-eyed veliger at hatching, four days post-deposition. Scales: B and C = $20 \mu\text{m}$.



C



cases. *Retusa obtusa* also usually exhibits an umbilical chink and a weaker or absent columellar fold.

The maximum shell length of 9 mm for *Acteocina canaliculata*, given by MARCUS (1977:14) and others, is in error, being attributable to *Bulla canaliculata* d'Orbigny, 1841, a probable synonym of *Tornatella bullata* Kiener, 1834.

Although current literature (ABBOTT, 1974) characterizes *Acteocina canaliculata* as a shallow-water, estuarine species, this viewpoint was derived from the incorrect results of WELLS & WELLS (1962). Our examination of live-collected museum specimens determined wider ecological and bathymetric ranges—from estuarine to oceanic, and from intertidal to a depth of 40 m.

Acteocina chowanensis Richards, 1947, is herein synonymized with *A. canaliculata* for the first time, based on examination of type material. *Tornatina coixlachryma* Guppy, 1867, is herein removed from synonymy with *A. wetherilli* (= *A. canaliculata*), as stated by DALL (1890) and PILSBRY (1921). The neotype of *T. coixlachryma* (USNM 369322), designated by WOODRING (1928), has a protoconch indicating direct development and spiral striae over the entire teleoconch; it does not agree in morphology with any of the species discussed herein.

In his synonymy of *Bulla* (*Tornatina*) *Wetherilli* [sic], DE GREGORIO (1890) listed “=(1887. *Tornatina crassiplicata* Conr. Meyer . . .).” This refers to *Bulla crassiplicata* Conrad, 1847, and to MEYER's (1887) listing and figure of that species. Both Meyer's figure and the lectotype (ANSP 13412) and paralectotypes (ANSP 13413) of *B. crassiplicata* exhibit cylindrical shells with keeled shoulders around low to nearly involute spires. This is very different from *A. wetherilli*; therefore, we also remove *B. crassiplicata* from synonymy with *A. wetherilli*.

FRANZ's (1971b) observations on larval development of *Acteocina canaliculata* from Connecticut compare well with our observations from eastern Florida. Franz noted oviposition only at night, while Florida specimens oviposited from 2400 to 1800; he also noted a smaller range (250–700) in the number of eggs per mass. Franz found sand grains adhering to the newly deposited egg mass; we observed this also, but found that most of the sand grains fell off within a few hours after deposition. Floridian *A. canaliculata* egg capsules were generally smaller, as was the diameter of the uncleaved ovum. The larval shell, at hatching, was also slightly smaller in Floridian specimens. Shell length at metamorphosis in Florida was identical to that found in Connecticut; however, metamorphosis occurred after 14 to 20 days post-hatching in Florida, twice as long as in Connecticut.

Acteocina candei (d'Orbigny, 1841)

(Figure 6)

Bulla candei D'ORBIGNY, 1841:128–129; 1842:pl. 4 bis, figs. 1–4.

†*Acteocina anetaspira* WOODRING, 1928:121–122, pl. 2, fig. 6.

†*Acteocina canaliculata vaughani* GARDNER, 1948:278–279, pl. 38, figs. 5–6.

Acteocina candei: WELLS & WELLS, 1962:87–93 (in part); figs. 4, 7–10, 12.

†*Acteocina elachista* WOODRING, 1970:418, pl. 62, figs. 1–2.

Material examined

Lectotype (designated herein): 3.28 mm specimen, BM(NH) 1854.10.4.17 (in part).

Paralectotypes (designated herein): 2.61 mm and 2.25 mm specimens, BM(NH) 1854.10.4.17 (in part).

Type material of synonyms:

†*Acteocina anetaspira* Woodring, 1928: holotype, USNM 369321. Bowden Formation, Miocene, Jamaica.

†*Acteocina canaliculata vaughani* Gardner, 1948: holotype, USNM 497059. Waccamaw Formation, Pliocene, North Carolina.

†*Acteocina elachista* Woodring, 1970: holotype, USNM 646052. Gatun Formation, Miocene, Canal Zone.

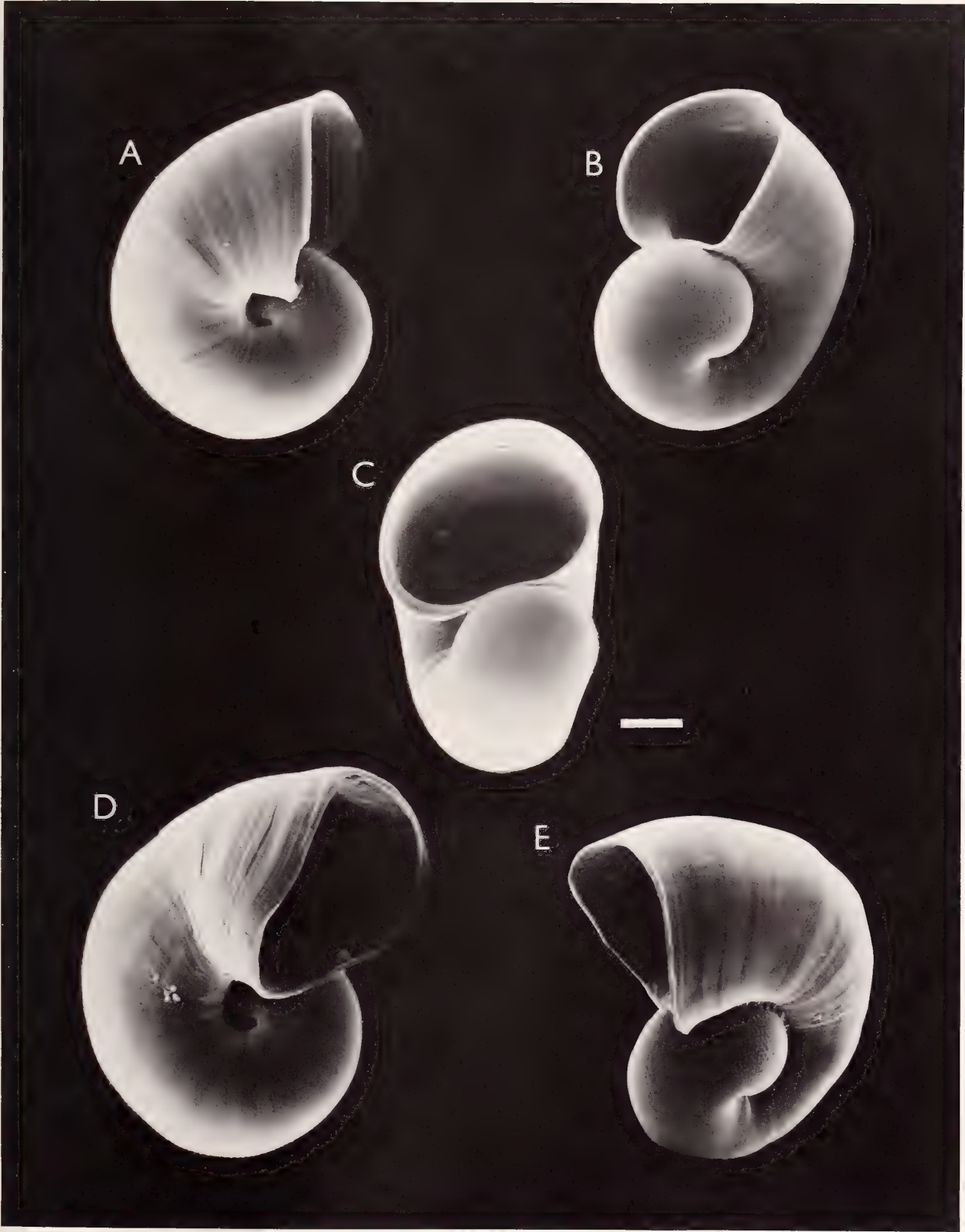
Other material: *North Carolina*: off Cape Hatteras: 14E, USNM 322831.—off Cape Lookout: 4L, UNC-IMS 9278.1–4.—*South Carolina*: 5L, R. Van Dolah Collection.—*Georgia*: off Savannah: 7E, UNC-IMS 7544.1–7.—*Florida*: off St. Augustine: 1E, IRCZM 65:1943.—off Miami: 2E, USNM 358309 (in part).—‘Tortugas’: 26L, USNM 358304 (in part).—off Sanibel Island: 4E, MCZ 245063.—off Calhoun County: 7E, ANSP 83825.—*Alabama*: off Mobile: 4E, USNM 323745.—*Texas*: off Galveston: 1L, HMNS 8133; 3E, HMNS 9266.—*Greater Antilles*: Northwest Cuba: 76L, USNM 358210 (in part).—Jamaica: 11E, USNM 442626.—*Haiti*: 2E, USNM 383220 (in part).—*Lesser Antilles*: British Virgin Islands: 6L, ANSP 338601.—*Antigua*: 23E, USNM 500363 (in part).—*Barbados*: 17E, USNM 500360 (in part).—*Grenada*: 24E, ANSP 296954.—*Bonaire*: 7E, ANSP 351033.—*Central America*: Yucatan: 6E, USNM 323195.—*Belize*: 1E, ANSP 20656.—*Limon Bay, Panama*: 1E, USNM 760350.—*South America*: Cabo Orange, Brazil: 13E, MORG 21.811.—Fernando de Noronha, Brazil: 12E, MORG 20.608.—Sao Paulo, Brazil: 31L, MORG 21.743.—Uruguay: 8E, MORG 20.070.—San Antonio, Argentina: 17E, MORG 17.917.

Original description

D'ORBIGNY (1841:128–129) originally described shells of *Bulla candei* as “oval, oblong, thick, slightly narrowing

Figure 5

Acteocina canaliculata, post-larval development. A, B, and C. Shell at metamorphosis. D and E. Shells at approximately one week post-metamorphosis. Scale = 50 μ m.





anteriorly, smooth, bright, marked slightly by a few lines of growth. Spire prominent, conical, canaliculate on the suture, aperture narrow, ending in a point posteriorly, very enlarged anteriorly, and supplied, on the columella, with a ridge resembling a tooth. Color uniformly white." d'Orbigny also described the general appearance of the hyperstrophic protoconch. No distinction was made between *B. candei* and the earlier described *Volvaria canaliculata*.

Type material

The type material of *Bulla candei* (Figures 6A, C) consists of three specimens (3.1, 2.5, and 2.1 mm lengths) glued to a strip of black paper. All three have intact protoconchs and appear to have been dead-collected. A fourth specimen originally part of the lot was found to be missing in 1982 by BM(NH) personnel, but is believed to have been the smallest of the four based on the size of its impression in the glue. We herein designate the largest specimen of the remaining three as lectotype (Figure 6A), because it most closely approximates d'Orbigny's illustration (1842:pl. IV bis, figs. 1–4; reproduced herein, Figure 6D) as well as the dimensions (3 mm long by 2 mm wide) given in the original description (D'ORBIGNY, 1841). The two smaller specimens are herein designated as paralectotypes. The type locality was given as the "Antilles."

Diagnosis

Shell, radula and gizzard plates as in *Acteocina canaliculata*, except: subsutural sculptural band strongly impressed with distinct axial ribbing; spire height usually greater than 20% of total shell length; shell shape more uniformly cylindrical.

Distribution

Cape Hatteras to peninsular Florida and entire Gulf coast to Texas; throughout the Caribbean, including the Greater and Lesser Antilles, coasts of Central America and South America to San Antonio, Argentina; recorded from 3 to 42 m.

Remarks

Acteocina candei is primarily an offshore species. From the appearance of its protoconch, it is probably planktic-developing. The adult shell is extremely similar to that of the planktic-developing, congener *A. canaliculata*. We are unable to distinguish the two species on the basis of shell

thickness, radula, gizzard plates, or gross reproductive anatomy. The only consistent diagnostic character for *A. candei* is the presence of a strongly impressed, and usually ribbed, subsutural band of sculpture (Figure 6F), apparently what D'ORBIGNY (1841) meant by "canaliculate on the suture." This subsutural band of sculpture is as reliable a conchological character to separate *A. candei* from *A. canaliculata* as are the involute spire and double columellar fold used to distinguish *A. bidentata* (D'ORBIGNY, 1841) from either *A. candei* or *A. canaliculata* (all three species have extremely similar radulae and gizzard plates). *Acteocina candei* also usually exhibits a more uniformly cylindrical (*i.e.*, less pyriform) shell shape, greater spire height, and a more highly protruded protoconch.

Acteocina candei and *A. canaliculata* were synonymized by MARCUS (1977). According to her illustrations, MARCUS (1977:figs. 39, 42a), also included a third species (described as new below). Whether both *A. canaliculata* and *A. candei* were actually present in Marcus' material cannot be reliably determined from her text or illustrations. The subsutural sculptural band below the suture in *A. candei* is distinct, consistent, and comprises a good specific character in our opinion. This is perhaps the same feature noted by D'ORBIGNY (1841) as "canaliculate on the suture," and by DALL (1922:96) as "channel at the suture." However, Dall probably considered specimens of both *A. candei* and *A. canaliculata* in observing that the "channel" varied from "clear-cut and sharp" (= *A. candei*) to "obsolete" (= *A. canaliculata*). Because of this distinct sculptural feature, we resurrect *A. candei* from synonymy, giving it full specific status. Until living specimens of *A. candei* can be further studied, the relationship between it and *A. canaliculata* is uncertain. Therefore, only a preliminarily revised diagnosis and distribution for *A. candei* are given herein; detailed description awaits more complete study.

Based on examination of their type material, the following fossil species are herein synonymized with *Acteocina candei*: *Acteocina anetaspira* Woodring, 1928 (synonymy previously suggested by WOODRING [1970]); *Acteocina canaliculata vaughani* Gardner, 1948; and *Acteocina elachista* Woodring, 1970.

Acteocina atrata

Mikkelsen & Mikkelsen, spec. nov.

(Figures 7–10)

Retusa canaliculata: WELLS & WELLS, 1962:87–93.

Utriculostris canaliculata: MARCUS, 1977:14–17 (in part), figs. 39, 42a.

Figure 6

Acteocina candei. A. Lectotype, 3.28 mm, BM(NH) 1854.10.4.17 (in part). B. Shell from offshore of Indian River region, 2.89 mm. C. Syntypes, BM(NH) 1854.10.4.17, glued to a strip of black paper; lectotype is at extreme left. D. D'ORBIGNY's (1842) original illustration. E. Same as B, "apical" view of protoconch. F. Same as B, posterolateral view of shoulder, showing sculptured subsutural band. Scales: E = 50 μ m; F = 100 μ m.

Utriculostraca canaliculata: MIKKELSEN & MIKKELSEN, 1982: 38 (in part).

Cylichnella canaliculata: MIKKELSEN & MIKKELSEN, 1983: 91.

Material examined

Holotype: (Figures 7A, B), 3.72 mm, USNM 838029.

Paratypes: 25 each to USNM 838030, ANSP A 10112, MCZ 294223, IRCZM 65:1996, BM(NH) 1983098, UNC-IMS 9860.1-25, HMNS 13002, CAS 035945, and MORG 22.549.

Type locality: Indian River lagoon, Indian River County, Florida; in shallow, subtidal mud east of Round Island, on the eastern side of the lagoon (Figures 7C, D), 27°33.53'N latitude, 80°09.91'W longitude. Salinity at the time of collection was 17 ppt.

Other material: Florida: St. Augustine: 10E, USNM 358292 (in part).—Turnbull Creek (vouchers): 11L, USNM 836098; 3L, IRCZM 65:2001.—Haulover Canal area (vouchers): 10L, ROM1Z B2463.—Merritt Island (Pleistocene fossils): 8E, USNM 371722; 8E, IRCZM 65:1999; 8E, PRI 30017a-h.—Round Island (vouchers): 24L, ROM1Z B2461.—Lantana: 61E, ANSP 357893.—Miami area: 193E, USNM 270719 (in part).—Sanibel Island: 70E, MCZ 282080-b.—Sarasota: 7E, USNM 36019.—Clearwater area: 2L, ANSP 357892.—Tampa Bay: 21E, ANSP 356485.—Cedar Keys: 13L, USNM 36020 (in part).—off Ft. Walton: 3E, MCZ 282779.—Bahamas: Great Abaco: 2E, ANSP 299498.

Diagnosis

Teleoconch thin-walled, cylindrical. Shoulder keeled, with a distinct subsutural, sculptural band. Protoconch globose, showing nearly straight suture in lateral view. Lateral radular teeth with one row of denticles directly on inner carinate edge of cusp. Unpaired gizzard plate heart-shaped. Tissues of gizzard, pallial caecum, and Hancock's organs black.

Etymology

The specific name *atrata*, from the Latin *atratus*, means "clothed in black" and refers to the black pigment present on various tissues of the living animal.

Distribution

Both sides of peninsular Florida; Bahamas (one record of dead shells from Great Abaco); less than 2 m. Uncon-

firmed literature record from Pamlico Sound, North Carolina (WELLS & WELLS, 1962).

Description

Shell characters

The heterostrophic shell of *Acteocina atrata* (Figure 8A) consists of a smooth, hyperstrophic, sinistral protoconch, followed by a cylindrical, orthostrophic, dextral teleoconch with up to three whorls in adults. The teleoconch is off-white, smooth, translucent, and more thinly shelled than that of *A. canaliculata*, with the shell wall approximately 112 μ m thick at the midpoint of the adult body whorl. The shell is angulate or keeled at the shoulder, and shows a prominent subsutural sculptural band. The aperture extends from 78 to 97% of the shell length, and flares widely at the rounded to truncate anterior end. In Indian River material, the shells reached a maximum length and width of 5.4 mm and 2.7 mm respectively, and varied in spire angle from 80 to 160 degrees and in spire height from 3 to 22%. Large shells (3 mm and over) showed a strong tendency for the last whorl to be set at an abnormally high level on the body whorl, thus decreasing the expected final spire height and increasing the expected final spire angle. Periostracum as in *A. canaliculata*. The protoconch (Figures 8E-G), when viewed "laterally" (either from the larval shell's umbilical or apical aspect) exhibits an only slightly curved suture. From its posterior view (Figure 8F), the protoconch is globose and does not taper. The percent of protoconch protrusion varied from 27 to 70%.

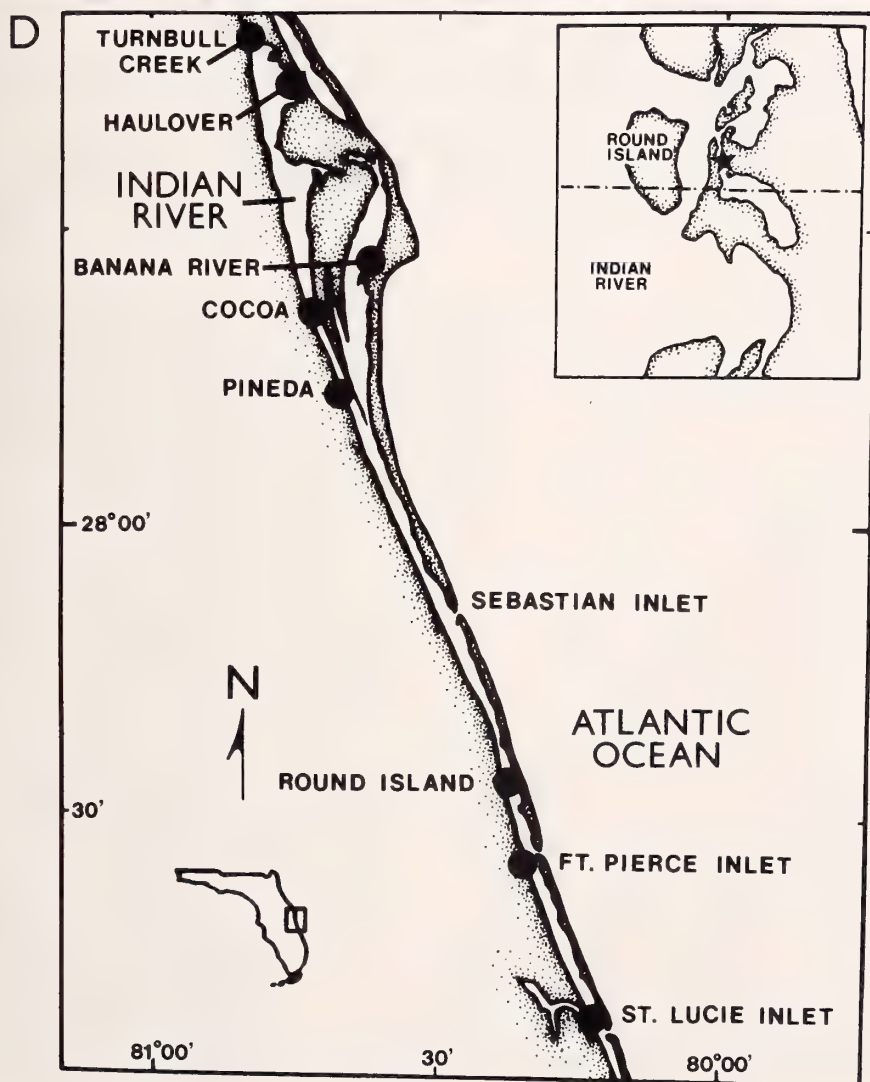
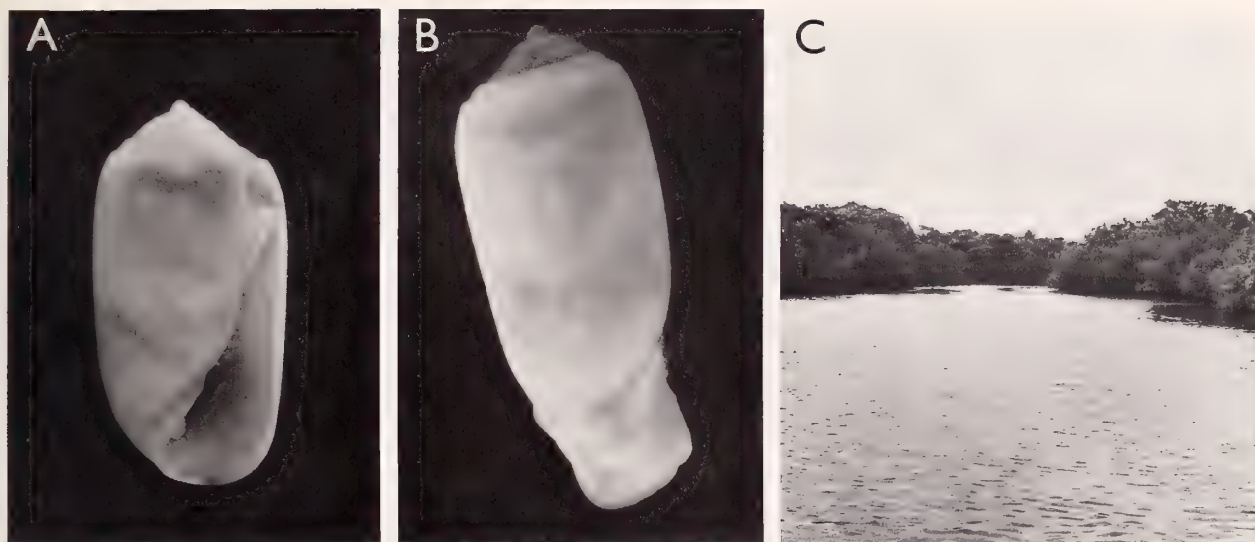
Correlation coefficients (r) for shell characters (Table 1) followed a pattern similar to those for *Acteocina canaliculata*.

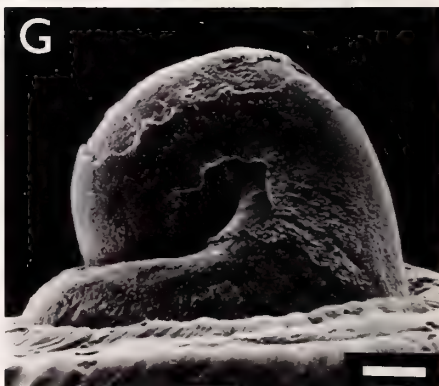
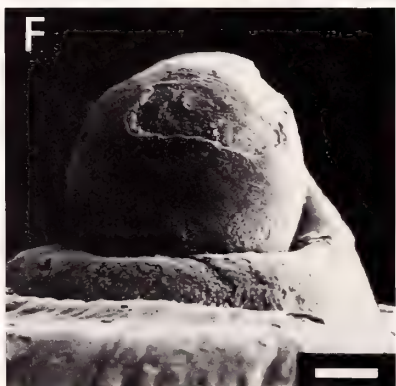
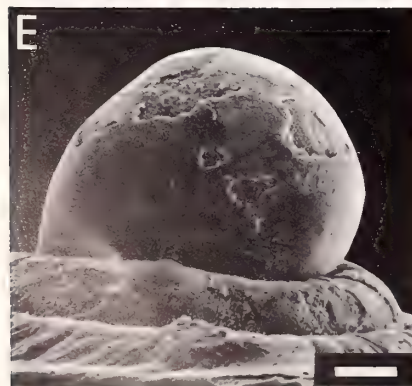
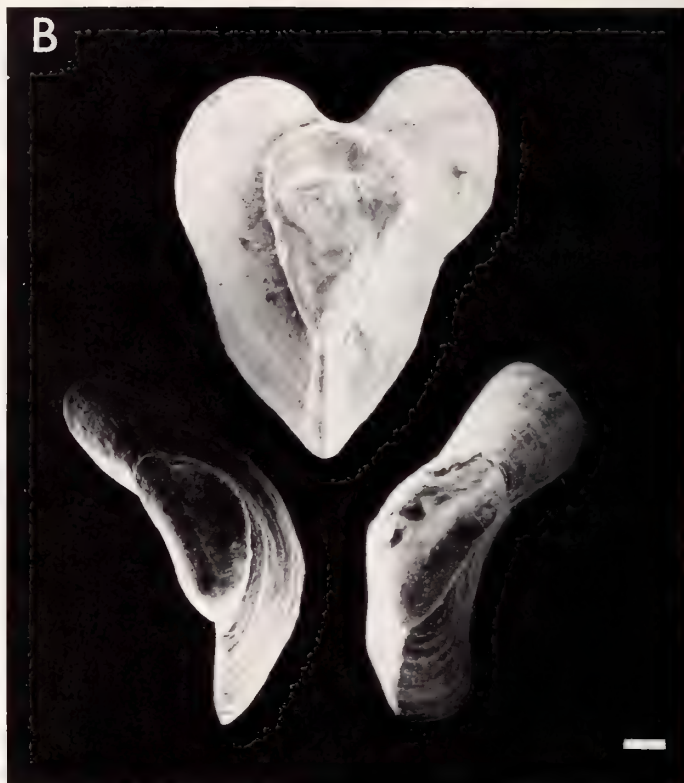
Radular characters

The radular formula of *Acteocina atrata* is 1-R-1, with 14-19 rows in specimens 2 mm or more in length. The rachidian teeth are centrally notched, with each rounded half bearing 5-11 sharply pointed denticles. The width of the rachidian teeth ranged from 24 to 39 μ m. The lateral teeth (Figures 8C, D) are distinct from *A. canaliculata*, being sickle-shaped, unicuspid, and bearing one row of finer denticles directly on the cusp's inner carinate edge. A blunt basal tubercle is present for articulation with adjoining lateral teeth. The lateral teeth varied ontogenetically in number of denticles from 14 to 25, in width from 46.8 to 97.8 μ m, and in angle from 98 to 125 degrees.

Figure 7

Acteocina atrata, spec. nov. A. Holotype, 3.72 mm, USNM 838029. B. Same as A, crawling animal. C. Round Island cove, the type locality of *A. atrata*. D. Map of the central east coast of Florida, showing primary collection sites (dots); detailed insert shows type locality (star), east of Round Island and north of the Indian River County/St. Lucie County line.





Variation within a single radula was also noted, especially in number of lateral tooth denticles. Hatchlings possessed radulae with 4–5 denticles per lateral tooth, increasing to 6 denticles in 14–20 days. These denticles are of the same form as those in the adult specimens, located directly on the inner carinate edge of the cusp; no wing-like expansion supporting the denticles, as is present in *A. canaliculata*, was seen at any stage of development.

Correlation coefficients (r) for shell length versus radular characters (Table 1) were generally low, with the exception of lateral and rachidian tooth widths, as in *Acteocina canaliculata*. However, lateral tooth width versus lateral tooth angle ($r = 0.60$) was an order of magnitude higher than in *A. canaliculata*; shell length versus lateral tooth angle was also notably higher.

Other features

The foot and mantle coloration in living *Acteocina atrata* is similar to *A. canaliculata*. The thinly walled adult shell of *A. atrata* allows visual observation of a portion of the internal anatomy, enhanced in this species by the presence of black pigment (absent in *A. canaliculata*) in the tissue over the gizzard and the pallial caecum (Figure 7B). Black pigment is also visible in the lateral groove between the cephalic shield and the propodium, in the vicinity of Hancock's organs.

The gizzard plates of *Acteocina atrata* are similar to those of *A. canaliculata*, except that the unpaired plate is distinctly heart-shaped (regardless of method of extraction, preparation, or degree of desiccation).

Gross reproductive anatomy was examined and found not to differ from that described by MARCUS (1977) and GOSLINER (1979) for *Acteocina canaliculata*. Preliminary observations by T. M. Gosliner (personal communication, 1983) determined differences in penial morphology between *A. atrata* and *A. canaliculata*.

Oviposition

Oviposition occurred in a time frame identical to that of *Acteocina canaliculata*. Spawning occurred monthly in the field and in the laboratory, giving no indication of reproductive seasonality in the Indian River lagoon.

Egg mass

The egg mass of *Acteocina atrata* (Figures 9A, A') is very similar in general shape and size to that of *A. canaliculata*. It is also gelatinous, ovoid to spherical (from 2.3

to 5.0 mm in maximum diameter, mean = 3.5 mm), and is anchored at the sediment surface by a mucous thread. When freshly deposited, the egg masses were always heavily coated with sand grains, which persisted for most of the developmental period, but most of which dropped off during the last 1–2 days before hatching. The uncleaved egg diameter ranged from 132.3 to 175.9 μm (mean = 151.6 μm), and each mass contained from 23 to 148 eggs (mean = 91.1 eggs/mass). Each egg was enclosed in an oval capsule about $320 \times 262 \mu\text{m}$ (range: $268\text{--}347 \mu\text{m} \times 235\text{--}288 \mu\text{m}$). The capsules were interconnected by chalazal material, and were also loosely packed into transparent tubes, $427.0\text{--}807.7 \mu\text{m}$ in diameter (mean = $609.4 \mu\text{m}$), irregularly coiled within the egg mass. There were no nurse eggs or auxiliary yolk-like material.

In contrast to *Acteocina canaliculata*, statistical analyses showed low correlation coefficients (r) for shell length versus egg diameter, mass diameter, and number of eggs/mass (Table 1).

Larval development

Acteocina atrata exhibits capsular metamorphic development (as defined by BONAR, 1978). Although the time between developmental stages varied among egg masses, development within an individual mass was well synchronized. Early cleavages resulted in a 2-celled stage at 3 h, 4 cells at 4 h, 8 cells at 5 h, and 16 cells at 6 h. Further development proceeded rapidly to a multicelled or blastula stage, and then to the heart-shaped gastrula by 20 to 25 h into development.

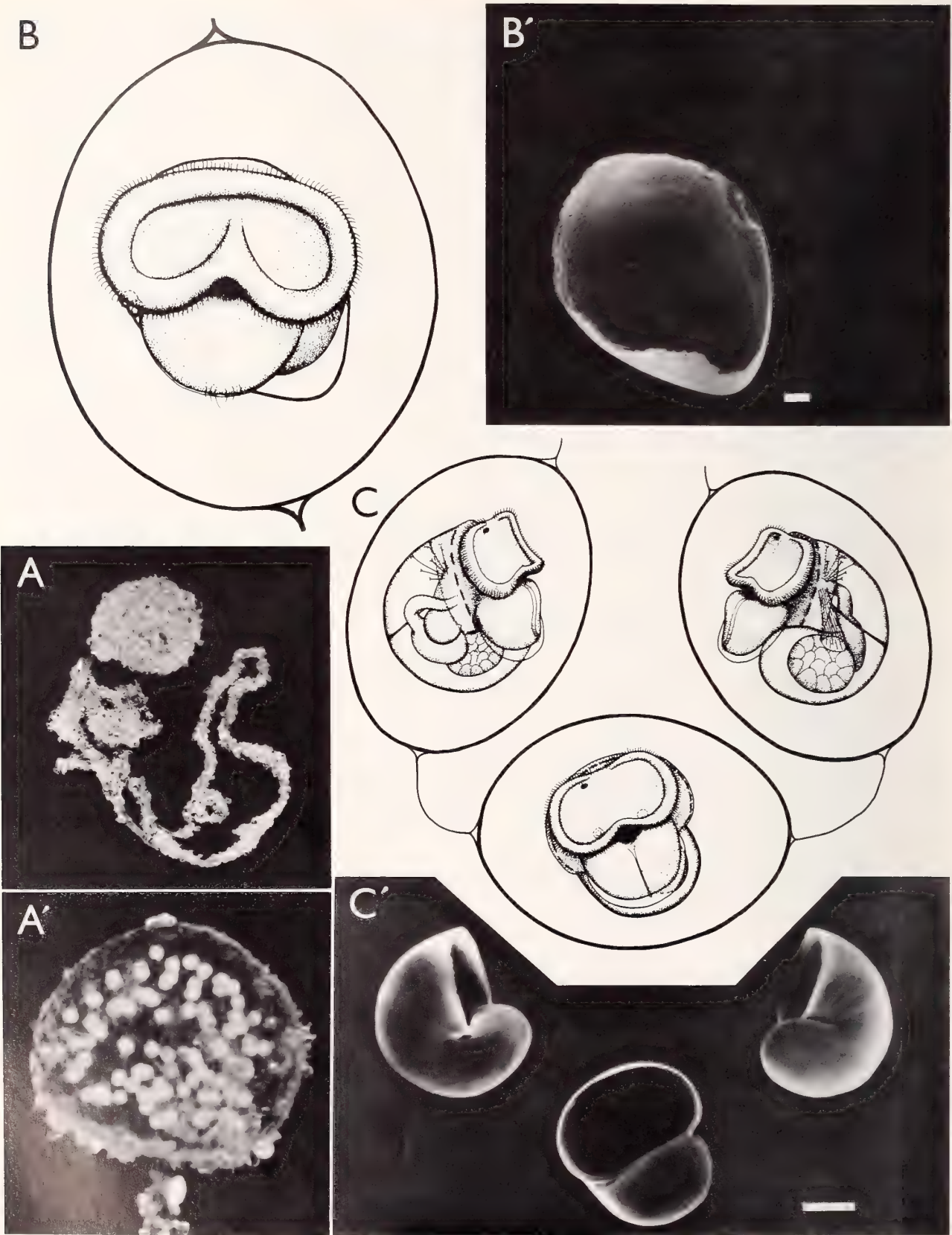
During the second 24-h period, the trochophore stage appears and begins to spin on its antero-posterior axis, 40–45 h into development. The mouth, metapodial rudiment, and prototroch bearing fine cilia are clearly visible at this stage; the vegetal pole appears as an undifferentiated spherical mass. Two anal cells are present on the lower right surface of the visceral hump.

The third day after deposition is characterized by a rapidly spinning, early veliger stage (Figures 9B, B'). A cone-shaped shell, 177 μm in length, has formed with its apex at the veliger's left. The velum is well formed, with a strong median elevation. The anal cells have migrated to a position below the lower right edge of the velum. A median ridge is evident on the rounded metapodium, and the operculum is visible at the edge of the foot. The viscera have begun to separate within the visceral hump.

By the fourth day, continued growth has modified the conical aspect of the larval shell, seemingly decreasing its

Figure 8

Acteocina atrata, spec. nov., adults. A. Shell from Indian River lagoon in apertural view, 4.18 mm. B. Gizzard plates, view of grinding surfaces. C. Outer edge of lateral radular teeth showing basal tubercle. D. Inner edge of lateral teeth showing denticles. E, F, and G. Protoconch: E. "Apical" view. F. "Posterior" view. G. "Umbilical" view. Scales: B = 100 μm ; C and D = 5 μm ; E, F, and G = 50 μm .



length to 165 μm . The direction of coiling from this point onward is decidedly skewed to the larval right. Spinning has slowed from the previous day, but continues steadily. The propodium has begun to expand. The digestive organs are clearly differentiated, as is a large, and now fully functional, retractor muscle on the larval left. The torsional process is represented solely by the migration of the anal cells, as in *Acteocina canaliculata*.

On day five, motion has slowed drastically although the larvae (Figures 9C, C') continue to turn, now frequently changing direction of rotation. The velar lobes are still fully extended, with the single row of fine preoral cilia erect and beating. No postoral band, or subvelum, has developed nor will develop in this species. The propodium has continued to develop and the median metapodial band is now a strong keel. A pair of otocysts has appeared in the base of the foot. A small right eye is visible.

The continued decrease of spinning movement and the appearance of the left eye, initially smaller than the right, occur on day six. As the larva stops rotation by day seven, the larval heart (at the center of the larva, just dorsal to the foregut) begins to pump. A mantle opening appears to the right of the cephalic area; at its edges beat cilia longer than those of the velum. Also as rotation ceases, the velum becomes reduced to form the cephalic shield of the juvenile snail, with its row of fine cilia still visible. The propodium is well inflated and nearly equal in size to the metapodium.

The larva of eight days, with a shell length of 260 μm , nearly fills its egg capsule, and spends much time fully retracted. A radula of four rows is present, with about four denticles on each lateral tooth. The osphradium and the two-chambered adult heart have formed in the mantle, appressed to the interior right side of the shell. As the continuous crawling movements that precede hatching begin on day nine, 200–210 h after deposition, the adult heart begins to beat. The egg capsules appear thin and weakened by this time, and the larvae break through them to crawl freely within the egg tubes. Nearly all of the larvae will have hatched from their capsules before breaks in the tubes and mass are located and benthic life can begin. At hatching (Figures 10A–D), shell length is 300 μm , the larval retractor muscle and operculum are still present, and there is no evidence of gizzard plates. In lateral view (Figure 10D), the short and only slightly curved suture line of the larval shell is distinct.

Immediately after hatching, shell growth becomes accelerated at the larval right, beginning the change in direction of coiling. The teleoconch first appears within the

apertural edge of the protoconch, creating a distinct suture. At the larval left, the leading edge of the teleoconch is still internal four days after hatching (Figures 10E, F). Starved hatchlings of similar age showed no trace of teleoconch growth. The operculum is lost during the second post-hatching week, and the black pigment characteristic of *Acteocina atrata* appears during the sixth week, at 0.75 mm shell length.

During the first 2–3 weeks after hatching, when the transition from sinistral to dextral coiling takes place, the increase in shell length is slow, gaining only about 0.01 mm/week. When this transitional phase of growth is completed, shell length increases at a mean rate of 0.11 mm/week under laboratory conditions; this rate of growth continues until a shell length of about 2.5 mm has been attained, approximately 23 weeks after hatching. At this time, increase in shell length again slows considerably.

Remarks

There is a possibility that *Acteocina atrata* is not properly placed in the genus *Acteocina*, because of distinct differences in the lateral radular teeth, specifically the absence of the denticle-bearing "wing." In this regard, the lateral teeth of *A. atrata* more closely approximate those of the types of *Tornastr*a and *Paracteocina* Minichev, 1966 (see MARCUS, 1977), than they do those of the type of *Acteocina*. Therefore, generic placement of *A. atrata* in *Acteocina* may be tentative, pending generic revision of the group.

Fossil specimens of *Acteocina atrata* have been recently discovered at a canal excavation site on Merritt Island, Brevard County, Florida. The Pleistocene fossiliferous layer was approximately 1.8 m under the surface. The specimens were found with roughly equal numbers of *A. canaliculata*. The venerid bivalve *Parastarte triquetra* (Conrad, 1846) was also present in great numbers, paralleling Recent conditions in the Indian River lagoon.

The development of *Acteocina atrata* is similar to that of *Retusa obtusa*, the only other cephalaspid with well-documented capsular metamorphic development (see SMITH, 1967a, b; BONAR, 1978). However, there are notable differences (*A. atrata* versus *R. obtusa*): a smaller egg diameter (151.6 versus 245 μm) and a greater number of eggs per mass (means of 91.1 versus 33 eggs, and maxima of 148 versus 46). In *A. atrata*, the entire developmental progression toward hatching is greatly accelerated at all stages. Hatching in *A. atrata* occurs 3.2 times faster: 9 days versus 29 in *R. obtusa*. Several anatomical differ-

←

Figure 9

Acteocina atrata, spec. nov., larval development. A. Egg mass with sand coating. A'. Same as A, enlarged slightly, with sand removed. B and C. Larval stages showing appearance of larvae corresponding to larval shells. B. Early veliger in egg capsule, three days post-deposition. B'. Same as B, shell only. C. One-eyed veligers in capsules, five days post-deposition. C'. Same as C, shells only. Scales: B and B' = 15 μm ; C and C' = 50 μm .

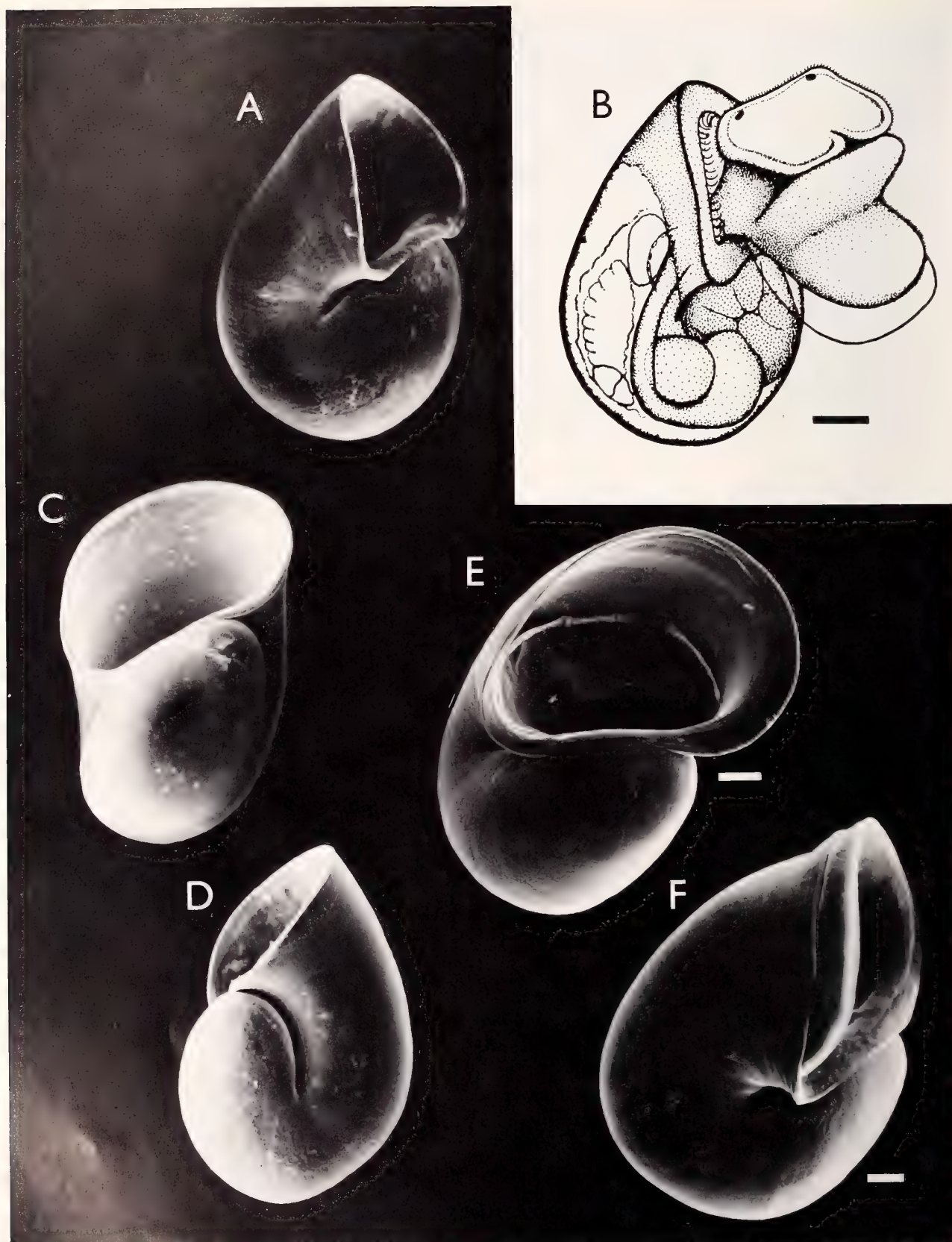


Table 2

Distinguishing characteristics of *Acteocina canaliculata*, *A. atrata* spec. nov., and *A. candei*.

	<i>Acteocina canaliculata</i>	<i>Acteocina atrata</i>	<i>Acteocina candei</i>
Egg mass	Sand-free Tubes absent Many (>150) small eggs	Sand-covered Tubes present Few (<150) large eggs	? ? ?
Development	Planktotrophic Florida: Hatch on day 4, settle on day 24 Connecticut: Hatch on day 4, settle on day 14–20	Capsular metamorphic Hatch on day 9, as benthic juveniles	Planktic (?) ?
Trochophore	Spins on lateral axis	Spins on antero-posterior axis	?
Veliger	Spherical early embryonic shell Pointed foot Subvelum present Long velar cilia	Cone-shaped early embryonic shell Rounded foot Subvelum absent Short velar cilia	? ? ? ?
Shell	Pyriform Rounded shoulder Thick-walled (175 μ m)	Cylindrical Keel shoulder Thin-walled (112 μ m)	Cylindrical Sculptured shoulder Thick-walled
Protoconch	Tapered Curved suture	Globular Straight suture	Tapered Curved suture
Gizzard	Pink-pigmented T-shaped unpaired plate	Black-pigmented Heart-shaped unpaired plate	Not pigmented (?) T-shaped unpaired plate
Lateral radular teeth	Denticles on wing of cusp Few denticles: 6–18 in adults	Denticles directly on cusp edge Many finer denticles: 14–25 in adults	Denticles on wing of cusp Few denticles

ences are also apparent. The initial appearance of the shell in the *R. obtusa* veliger is rounded and globular (SMITH, 1967b), not distinctly cone-shaped as in *A. atrata*. The larval kidney adjacent to the anus and the ciliated mid-velar groove of *R. obtusa* are both absent from *A. atrata* larvae. Also, the right larval retractor muscle of *R. obtusa*, composed of various muscle fibers to the right posterior interior of the shell, was not noted in *A. atrata*, although numerous small bundles attached to various dorsal and posterior locations were present. In addition, the prominent eyes, presence of a radula, pulsating larval heart, and median metapodial keel of *A. atrata* were not noted by SMITH (1967b) for *R. obtusa*.

Although we once considered the possibility of poecilogony for *Acteocina canaliculata*, the consistent differences in egg, larval, and adult characters (Tables 2, 3) indicate the definite presence of two distinct species. Preliminary electrophoretic examination (unpublished data, M. J. Harszewych, January 1983) of *A. canaliculata* and *A. atrata* has shown strong and consistent differences in their esterase systems, with strong tendencies in other enzyme systems as well.

DISCUSSION

Because most lots of *Acteocina canaliculata* in early museum collections are now known to have been correctly identified, the recent taxonomic confusion between *A. canaliculata* and *A. candei* apparently stems from WELLS & WELLS (1962). Although their conception of *A. candei* was correct, their "*Retusa canaliculata*" was in fact *A. atrata*; the true *A. canaliculata* seems to have been excluded entirely. FRANZ (1971b:181) was correct in his identification as well as in his belief that Wells & Wells' observations of direct development in *A. canaliculata* were for "some other cephalaspid." Our own earlier work reflects the taxonomic problems initiated by WELLS & WELLS (1962) and augmented by MARCUS (1977), who considered *Acteocina canaliculata*, *A. candei*, and *A. atrata*, all as a single species. While considering Marcus' synonymy valid, we (MIKKELSEN & MIKKELSEN, 1982) determined "*A. candei*" (actually *A. canaliculata*) to be a juvenile form of "*A. canaliculata*" (actually *A. atrata*). This incorrect result is now known to have been influenced by the coincidental lack at that time of large specimens of *A. atrata*. After

Figure 10

Acteocina atrata, spec. nov., post-larval development. A, C, and D. Shell at hatching. B. Appearance of hatchling corresponding to shell in A. E and F. Shells at four days post-hatching, showing unequal growth of teleoconch. Scales: A–D = 50 μ m (marker at B); E and F = 25 μ m.

Table 3

Results of *t*-tests to determine distinctness of the means of character distributions between *Acteocina canaliculata* and *A. atrata* spec. nov. (* indicates characters useful in distinguishing these species).

Significantly distinct		Significantly indistinct	
Character	P<	Character	P<
Spire angle	0.0001	Shell length	0.7627
Spire height	0.0022	Shell width	0.1755
Radular rows	0.0003	% Protoconch protrusion	0.7895
Lateral tooth denticles	0.0000	Egg mass diameter	0.2929
Rachidian tooth denticles	0.0010		
Lateral tooth width	0.0000		
Rachidian tooth width	0.0000		
Lateral tooth angle	0.0000		
*Number of eggs	0.0000		
*Egg capsule length	0.0000		
*Egg capsule width	0.0000		
*Egg diameter	0.0000		

larval development studies had convinced us of the presence of two distinct species (while still confusing the names), we suggested the resurrection of *A. candei* as a valid species (MIKKELSEN & MIKKELSEN, 1983). It was not until type material was examined that we determined the distinct characteristics for these species, and the correct identifications of our specimens.

Our search for previous names for *Acteocina atrata* included investigation of *Bulla pusilla* Pfeiffer, 1840. Personnel of the British Museum (Natural History) and the Museum für Naturkunde der Humboldt-Universität zu Berlin agreed that Pfeiffer's types were probably destroyed in the Stettin museum during World War II. This opinion was also held by DANCE (1966:197, 285). The Humboldt museum located a lot of 33 specimens of "*Bulla pusilla*" from Cuba in R. W. Dunker's collection, which were presumably obtained from Pfeiffer. This lot included 32 specimens of *Acteocina candei* and one specimen of a species of *Acteon*. However, in view of the uncertain status of this lot, the lack of definite type material, and the ambiguity of the original description, it is unknown what Pfeiffer intended to be called *Bulla pusilla* and the name must be considered a *nomen dubium*.

Analysis of *Acteocina canaliculata* and *A. atrata* from the Indian River lagoon showed overlap of all shell and radular meristic and morphometric characters (Figures 11, 12). Results of *t*-tests (Table 3) showed some significantly distinct means of the character distributions; how-

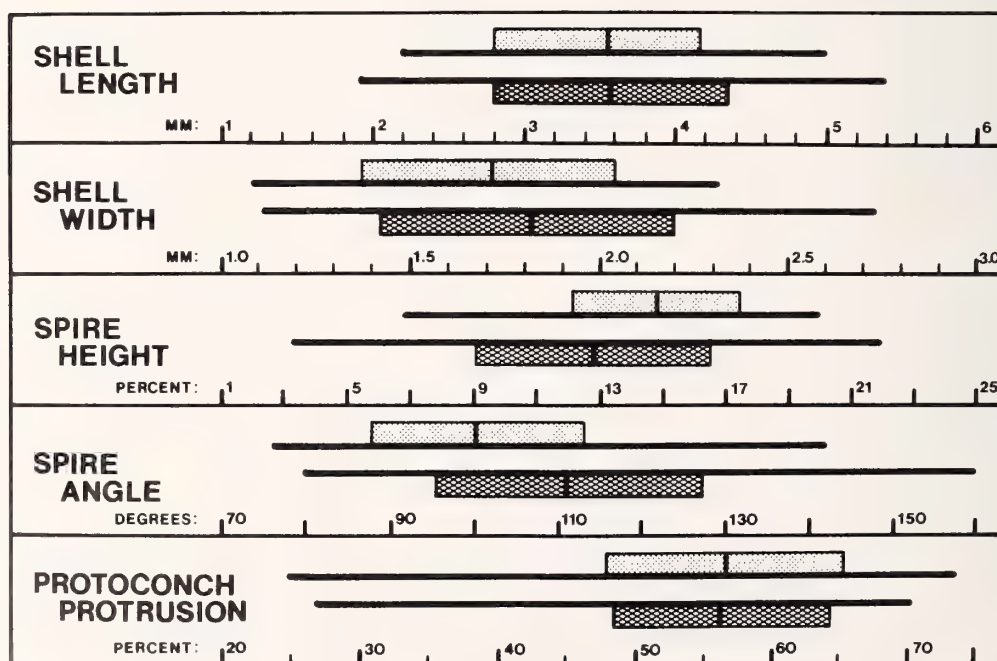


Figure 11

Variation in shell characters of *Acteocina canaliculata* (stippled; n = 56) and *A. atrata* (cross-hatched; n = 49). Ranges (horizontal solid line), means (vertical mid-point of pattern), and \pm SD (pattern) are plotted.

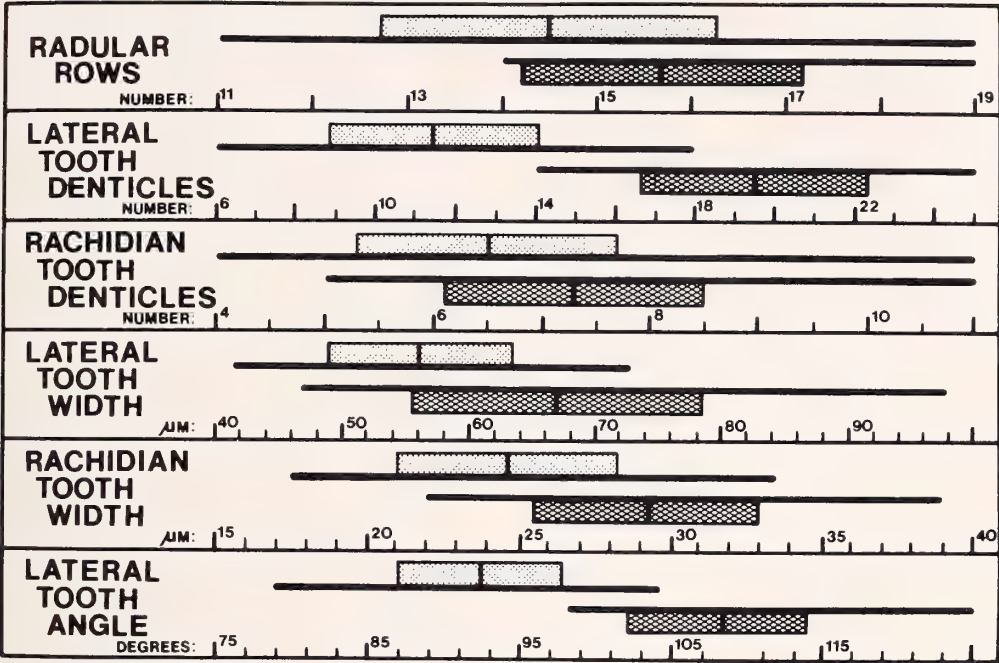


Figure 12

Variation in radular characters of *Acteocina canaliculata* (stippled; n = 56) and *A. atrata* (cross-hatched; n = 49). Symbols as in Figure 11.

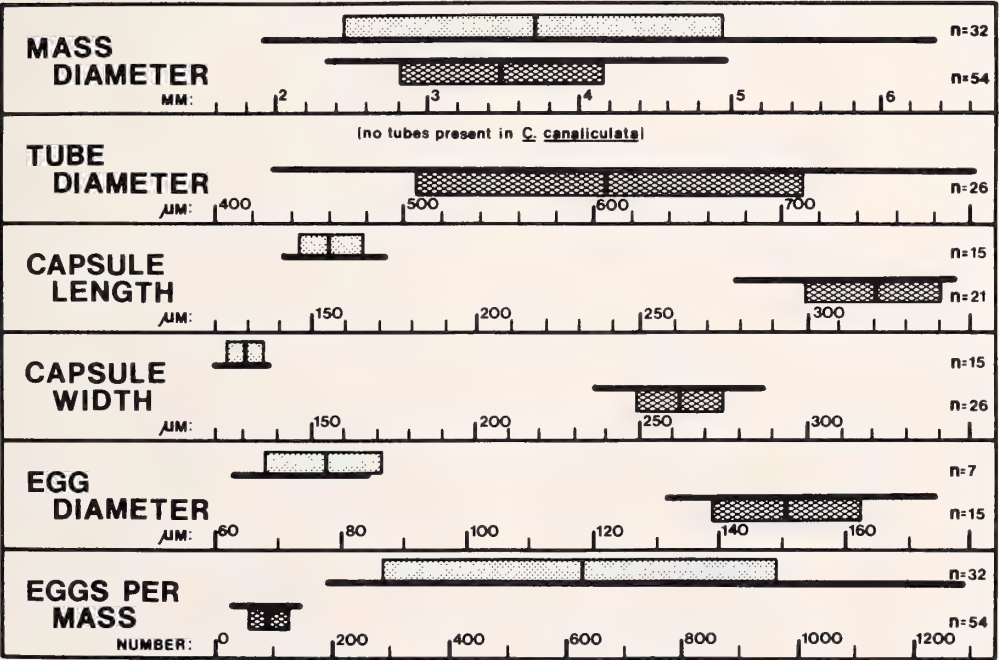


Figure 13

Variation in eggs and egg mass characteristics of *Acteocina canaliculata* (stippled) and *A. atrata* (cross-hatched). Symbols as in Figure 11.

ever, because of the overlap of the ranges, these characters cannot be reliably used in specimen identification. Consistent subjective differences do exist in the sculpture of the shoulder, the shape of the protoconch, the presence or absence of black pigment on the animal, the placement of lateral tooth denticles, and the shape of the unpaired gizzard plates. However, distinct meristic and morphometric differences exist in the characteristics of the eggs and egg capsules (Figure 13, Table 3).

The distinguishing characters for *Acteocina canaliculata*, *A. atrata*, and *A. candei* are summarized in Table 2. The most useful of these in the routine sorting of samples are the shape of the protoconch, features of the shoulder, and the presence or absence of black pigment on portions of the animal. Caution is advised, however, in the frequent cases where the protoconch is either worn or absent, or where the tissue has been stained or preserved. Also, potentially misleading black coloration may occur in the digestive gland of individuals of *A. canaliculata* that have been feeding on a blackish food source. This coloration, however, is restricted to the digestive gland and does not affect the areas of the gizzard, pallial caecum, or Hancock's organs.

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Pseudo-operculate Pulmonate Land Snails from New Caledonia

by

ALAN SOLEM

Department of Zoology, Field Museum of Natural History,
Roosevelt Road & Lake Shore Drive, Chicago, Illinois 60605

SIMON TILLIER

Laboratoire de Biologie des Invertebrates Marins et Malacologie,
55, Rue de Buffon, 75005 Paris, France

AND

PETER MORDAN

Department of Zoology, British Museum (Natural History),
Cromwell Road, London SW7 5BD, United Kingdom

Abstract. Two genera of New Caledonian land snails, *Pararhytida* Ancey, 1882 and *Rhytidopsis* Ancey, 1882, have a thick oval mass of densely compacted connective tissue formed on the dorsal side of their tail. This functions as an operculum to block the shell aperture when the animal retracts, and is named the pseudo-operculum. They are the only pulmonate land snails to have evolved a functional equivalent of the prosobranch operculum. *Pararhytida* inhabits dense leaf litter on the ground, while *Rhytidopsis* is an arboreal genus. Shells of both genera are very large compared with other charopid genera. The pseudo-operculum may have evolved under predation pressure from the large New Caledonian carnivorous land snails belonging to the genera *Ouagapia* Crosse, 1894 and *Ptychorhytida* Möllendorff, 1903 (family Rhytididae), and may have an exaptive value for size increase in leaf litter and for colonizing arboreal habitats in New Caledonian rain forests.

INTRODUCTION

THE PRESENCE of a horny or calcareous disk on the dorsal surface of the tail is one of the most obvious characters separating the prosobranch gastropods from the pulmonates. Among the latter, larval stages of the marine Onchidiidae (FRETTER, 1943), Otinidae, Ellobiidae, and Amphibolidae (HUBENDICK, 1978) retain the operculum, but it persists in adults of only two genera of Amphibolidae, *Salinator* Hedley, 1900 and *Amphibola* Schumacher, 1817. No land or fresh-water pulmonates have an operculum.

The fresh-water and terrestrial prosobranchs use the operculum both as a means of retarding water loss and as defense against predators. The effectiveness of the oper-

culum as a seal in excluding environmental dangers is shown by the example of the fresh-water prosobranch *Pomacea cumingii* (King & Broderip, 1831) from Panama, whose relatively thin and horny operculum permitted survival through a more than one hour immersion in a standard alcohol-formalin amphibian killing solution (NETTING, 1936). Many terrestrial prosobranch genera independently have evolved accessory breathing tubes in the shell itself to permit gas exchange during diapause (REES, 1964:58-65, pls. 3-5), as their calcareous opercula provide extremely tight-fitting seals.

In most terrestrial pulmonates, defense against predators and retardation of water loss are functionally separated. Pulmonates secrete a sheet of mucus across the ap-

erture which may retard water loss during diapause. This sheet may or may not be heavily calcified, and may be with or without a special breathing pore. Various structural and behavioral characteristics are used in defense against predation. Among the structural modifications may be development of a thick shell to defeat gnawing, provision of internal apertural barriers to prevent ingress by small arthropods (SOLEM, 1972), or sealing of the shell to a rock or piece of wood with mucoid cement so that removal requires considerable force. Nearly all members of the family Clausiliidae make use of a special structure, the clausilium, in addition to large apertural barriers, to close the aperture. Evolution of this structure from a columellar barrier that became detached has been postulated by NORDSIECK (1982). Shell color patterns may be effective in confusing potential predators (CAIN, in press). Behavioral adaptations include habitat shifts such as nightly tree climbing to avoid a nocturnal ground foraging predator, or day-time retreat into narrow crevices to avoid a diurnal predator. A few pulmonate species are known to secrete mucus-containing irritating chemicals, for example *Liguus* (EISNER & WILSON, 1970). The endemic ant *Camptonotus* was found to be repelled by *Liguus* mucus, but the introduced fire ant *Solenopsis geminata* (Fabricius) is successful in feeding on *Liguus* (TUSKES, 1981). Other species, such as *Sultana sultana* (Dillwyn, 1817), have a very sticky mucus that will engulf small predators (TILLIER, 1980:71). Veronicellid slugs in Samoa are a major problem to chicken owners, as their mucus can kill the fowls (SOLEM, 1971).

Only one other land pulmonate has been reported previously to have a mechanical device for shell closure, the enigmatic *Thyrophorella thomensis* Greeff, 1882 from Sao Thomé. This species is described as having a loose flap of the shell, connected only to the upper palatal margin of the shell lip, that can fall down over the aperture and then later be pushed up by the extending snail (GREEFF, 1882, 1884; GIRARD, 1893, 1895). The flap itself is not attached to the snail's body, and thus is not homologous to the operculum, nor can it function as a tight seal. Only fragmentary data have been published on the anatomy of *Thyrophorella* (above references), and whether it actually should be a monotypic family, as customarily listed, is uncertain. We have been unable to find later references to collections of this species, and the materials taken by Newton and reported on by GIRARD (1893, 1895) probably were destroyed in the fire at the Museu Boçage in Lisbon several years ago. Pending collection of new material and detailed anatomical study, this species will remain a puzzle.

The discovery that two genera of New Caledonian pulmonate land snails have a "pseudo-operculum" developed on the dorsal side of their tail is of general interest. When the snail is retracted into the aperture (Figure 1), this structure effectively blocks the opening and thus functions in an analogous way to a prosobranch operculum.

OCCURRENCE OF THE PSEUDO-OPERCULUM

The described land snail fauna of New Caledonia numbers only about 110 species (FRANC, 1957; SOLEM, 1961), but recent collections by P. Bouchet, P. Mordan, L. Price, A. Solem, A. Tillier, S. Tillier, and assistants indicate an actual diversity level of 300–400 species (Tillier, in TILLIER & CLARKE, 1983). The dominant group in terms of species numbers is the Charopidae (*sensu* SOLEM, 1983; listed as Endodontidae by FRANC, 1957, and SOLEM, 1961). More than half of the described New Caledonian land snail species belong to the Charopidae. New discoveries probably will increase this proportion.

Two charopid genera, *Rhytidopsis* Ancey, 1882 and *Pararhytida* Ancey, 1882, currently being revised (Tillier & Mordan, in preparation), share development of the pseudo-operculum and unique structures in the terminal female genitalia. Preserved specimens are available now for most other New Caledonian charopids, but no trace of a pseudo-operculum has been seen by the authors in any other taxa. Once seen and recognized, it will not be forgotten, although two malacologists who reported on the anatomy of *Pararhytida dictyodes* (Pfeiffer, 1847) surprisingly did not mention it (FISCHER, 1875; STARMÜHLNER, 1970:302–305).

Rhytidopsis chelonites (Crosse, 1868) is the only described species correctly assigned to *Rhytidopsis* (Tillier, unpublished results). *Rhytidopsis* ranges from Mt. Humboldt, somewhat north of Nouméa, to the southern tip of New Caledonia. In recent years, living specimens have been collected in rain forests at 150 to 1350 meters elevation, always from tree trunks or from the underside of leaves. The shell is relatively small (diameter 6–8 mm), flammulated to dotted in color pattern, and without major sculpture; the umbilicus is minute, and the shell slightly carinated at the periphery. Other taxa traditionally assigned to *Rhytidopsis* on the basis of general conchological similarity (see FRANC, 1957; SOLEM, 1961) also are arboreal, but have very narrow and elongated tails with a prominent caudal horn, often strongly sculptured shells, and no trace of a pseudo-operculum. Eventually they will be transferred into other genera.

Pararhytida, as revised by Tillier & Mordan (in preparation), excludes the taxa *Micromphalia* Ancey, 1882 and *Plesiopsis* Ancey, 1888. It includes six species, several of them new. *Pararhytida* ranges throughout the main island of New Caledonia and the Belep Islands, but is absent from the younger Loyalty Islands. Old records from the Isle of Pines have not been confirmed in recent decades. *Pararhytida* is found in most forest patches, excluding the high altitude rain forests and the very dry lowland forests. The largest species, *Pararhytida dictyodes* (Pfeiffer, 1847), ranges over the entire island and is quite variable. It is possible that it includes a complex of cryptic species. The remaining taxa show restricted ranges that correlate with



Figure 1

Retracted specimen of *Pararhytida dictyodes* showing functional position of the pseudo-operculum (Photograph by A. Solem).

particular rainfall regimes (Tillier & Mordan, in preparation). All species of *Pararhytida* are litter dwellers, and they are especially common inside the sheath portions of fallen palm fronds. They have not been taken under logs or in the rotting wood habitats utilized by other New Caledonian charopids. In most species the shell is sharply carinated and the umbilicus is wide. Adult shell diameter within *Pararhytida* is from 14 to almost 37 mm.

Thus, *Rhytidopsis* and *Pararhytida* differ in shell shape, size, ecology, and geographic range. Their monophyly is suggested by their unique pseudo-opercula and structures in the terminal genitalia.

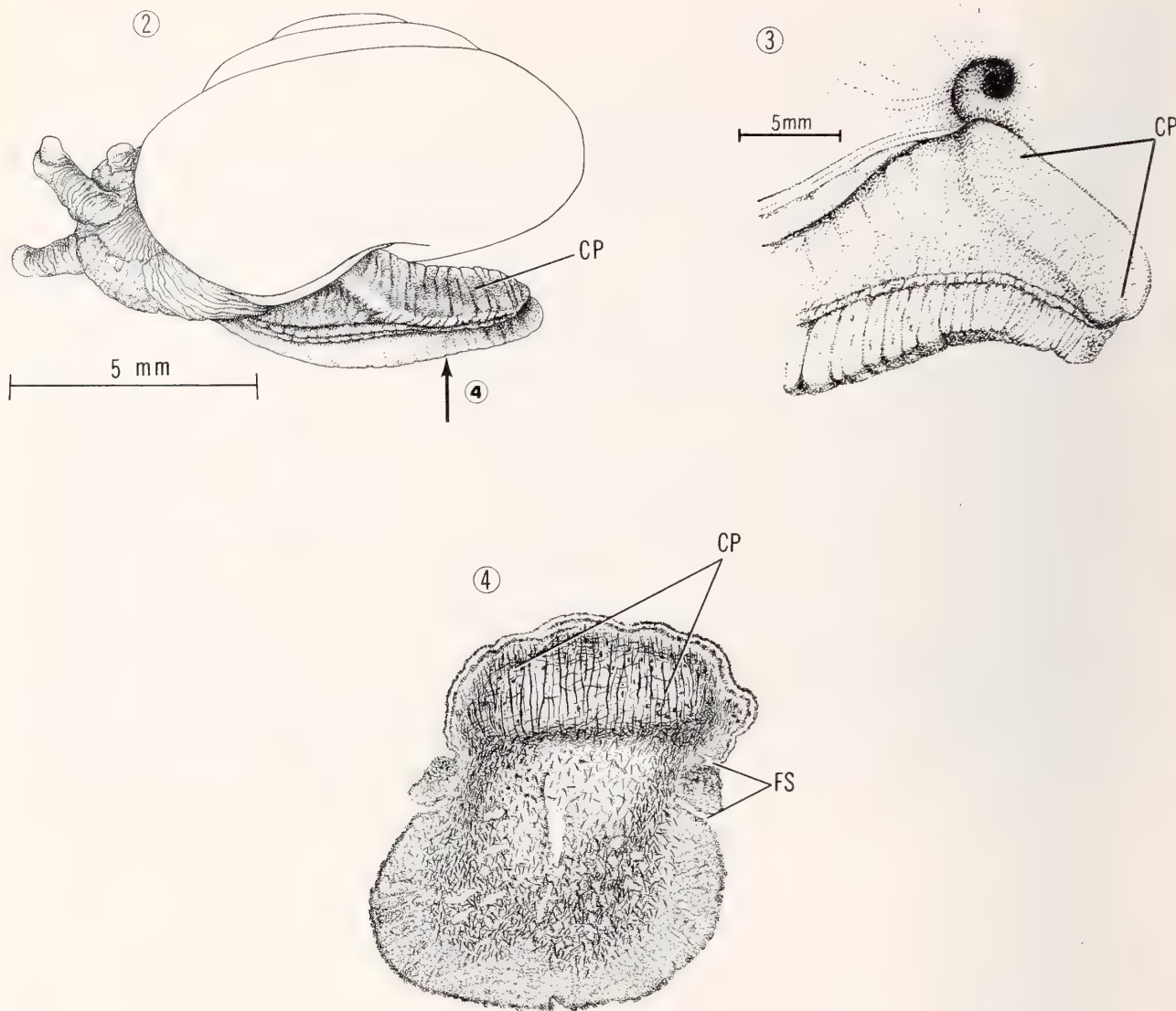
STRUCTURE AND FUNCTIONING OF THE PSEUDO-OPERCULUM

In both *Rhytidopsis* (Figure 2) and *Pararhytida* (Figure 3) the tail is relatively short and broad. The dorsal portion is clearly flattened and expanded into an elongately oval disk that extends from the visceral stalk to the tip of the tail. Its posterior margin can be rounded or narrowly tri-

angular, and varies individually. This novel structure is here named the pseudo-operculum.

The pseudo-opercula of two species of *Pararhytida*, *P. dictyodes* and *P. mouensis* (Crosse, 1868), have been examined histologically in longitudinal and transverse section, and are essentially similar in structure. The pseudo-operculum is composed of a thick pad of irregularly interwoven fibers underlying a single layer of epidermis. Staining with Masson's trichrome shows these fibers to be composed of collagen. The pad extends from just above the supra-pedal grooves to the top of the tail. It is extremely difficult to cut and almost impossible to tear. While the covering epithelium can be ruptured very easily, and was lost from much of the histological material studied here, the fibrous layer resists disturbance.

In section the pseudo-operculum may be broadly divided into two regions, which appear more sharply differentiated in *Pararhytida mouensis* than in *P. dictyodes*. Immediately below the epidermis lies a dense mass of collagen fibers with only a very few weak muscles. Beneath this is a rather more deeply staining layer of collagen, containing



Explanation of Figures 2 to 4

Figure 2. Preserved specimen of *Rhytidopsis chelonites* from Col de la Pirogue, Mont Mou, New Caledonia showing pseudo-operculum. FMNH 144272. Collected January 23, 1962.

Figure 3. Preserved specimen of *Pararhytida dictyodes* from Col

de la Pirogue, Mont Mou, New Caledonia showing pseudo-operculum. FMNH 135440. Collected January 25, 1962.

Figure 4. Cross-section through tail of *Rhytidopsis chelonites* (FMNH 144272) showing pseudo-operculum (CP) and pedal grooves (FS).

numerous muscle fibers, which, in the main portion of the pseudo-operculum, have a predominately dorsoventral orientation. These muscles extend well beyond the pseudo-opercular pad into the tail proper, where the fibers run mainly in the longitudinal plane (Figure 5). It is clear from the preparations stained with Alcian blue that, unlike the usual exposed epidermis of pulmonates, the surface of the pseudo-operculum is devoid of mucocytes and other secretory cells.

When the animal retracts into the shell, the dorsal part of the tail angles across the plane of the aperture, with its posterior tip on the outer palatal wall and the anterior section against the parietal margin (Figure 1). The pseudo-operculum thus effectively fills the shell aperture. This functioning implies that the pattern of retraction of *Pararhytida* and *Rhytidopsis* into their shells is different from the pattern observed in most terrestrial pulmonate snails. In the latter, the tail itself is retracted until its posterior



Figure 5

Transverse section through tail of *Pararhytida dictyodes* from Mt. Canala, New Caledonia, 900–1050 m, New Caledonia. Collected January 21, 1979. Magnification 31.5 \times .

tip lies above the pallial border. Space for this is provided by the lateral outward compaction of the lung cavity. Consequently only the mantle border is exposed in the plane of the aperture, and can thus secrete an epiphragm to separate the snail from the outside world. In both *Pararhytida* and *Rhytidopsis*, the tail remains distal to the pallial border, which may be related to the fact that the pseudo-operculum functionally replaces the epiphragm. Charopids and endodontids both secrete thin mucus sheets, and even taxa from drier Australian areas are not known to have calcareous thickening of the epiphragm (Solem, personal observations).

Although the exposed epithelial layer of the pseudo-operculum would be subject to evaporative water loss, presumably overall permeability would be reduced by the fibrous layer underneath. Instead of water passing freely from the entire tail surface to the exposed areas, it would have to flow around the edges of the pad, and, thus, less water would reach the evaporative surface itself. Contraction of the dorsoventral muscles in the pseudo-operculum could serve to expand the pad laterally and thus provide a better fit in the aperture. The exposed epithelial surface probably functions in respiration, since air flow to

the lung cavity would be severely impeded by the pseudo-operculum. It is also possible that the epidermis itself could actively reduce evaporative water loss, as has been shown in some European helicids (MACHIN, 1974; NEWELL & APPLETON, 1979).

The extent to which the pseudo-operculum gives actual protection against predation cannot be evaluated at present, but clearly the presence of a thick collagen fiber layer is potentially of great protective value. Rhytidids have been observed feeding on *Pararhytida* (Tillier, personal observations), but no analysis of rhytidid diets in New Caledonia has been attempted.

EVOLUTION OF THE PSEUDO-OPERCULUM

Geologically, New Caledonia is a fragment of the eastern border of Gondwana, which split off northeastern Australia during the Triassic, approximately 230 million years ago. It was possibly covered subsequently by two marine transgressions, but has been constantly exposed land since at least the Oligocene, or about 30 million years (PARIS & LILLE, 1977). As a result of this long isolation and existence as elevated land, the whole primary land snail fauna of New Caledonia is endemic at the specific level and many genera also are limited to New Caledonia.

The numerically dominant land snails of the family Charopidae show specializations in comparison with charopids elsewhere. The arboreal element is much better represented, and by far the largest species of Charopidae are found in New Caledonia.

A survey of body types in New Caledonian charopid land snails suggests a basic form dichotomy into (1) taxa with narrow, elongated tails that end in a prominent mucus pore and often a caudal horn, such as is common in the New Zealand otoconchine charopid genera (CLIMO, 1969:figs. 5A–F, 1971:figs. 1A–D) and (2) taxa with fairly short, often truncated tails, such as are found in typical Pacific Basin charopids (SOLEM, 1983:26, fig. 9a). The former tend to be arboreal in habits, the latter tend to be ground dwellers. Taxa of the *Rhytidopsis-Pararhytida* clade belong to the second morphological group, and are the only identified clade to be both arboreal and terrestrial.

The entire New Caledonian radiation of charopids is marked by a tendency towards large size, and *Pararhytida* includes the largest of all known charopids. Carnivorous land snails in New Caledonia reach moderately large size, *i.e.*, the 12–25 mm in diameter *Ptychorhytida* Möllendorff, 1903 and the 30–35 mm *Ouagapia raynali* (Gassies, 1863). These rhytidids are ground dwellers, and the large, litter-dwelling charopids would be logical prey for them. We do not know whether they feed exclusively on *Pararhytida*, but, as mentioned above, *Ouagapia* has been observed to feed on *Pararhytida*. The latter's habit of resting in the curled sheath portion of fallen palm fronds, not tightly sealed to the sheath surface, combined with the relatively large aperture of its shell, would leave the animals easy

victims for predatory ground snails. Any thickening of the exposed portion of the retracted animal that might discourage a feeding attempt would have selective value. Intensification of this trend would lead to the evolution of the pseudo-operculum. Because *Pararhytida* tends to be absent from the drier forests, we hypothesize that the pseudo-operculum functions primarily against predation.

Retardation of water loss would be a secondary benefit that might permit some members of the clade to utilize arboreal habitats, which are subject to greater humidity fluctuations, without any more morphological modification of the foot and lung cavity. The primacy of predation as a selective pressure in the evolution of the pseudo-operculum may find some confirmation from observations on the only terrestrial snails known to us that exhibit a pattern of animal retraction that is intermediate between the usual pattern and that found in the pseudo-operculate taxa. The large, African ground dwelling achatinids, for example *Achatina fulica* (Bowditch, 1822), when disturbed, do not retract their tail above the pallial border, but twist the tail so that its left side blocks the aperture, with the tip of the tail at the parieto-palatal margin (Binder, personal observation; also present authors). Subsequent full retraction and epiphragm building occurs in achatinids, so that this is not fully comparable, but this parallel behavior in an unrelated group is of interest. This use of the tail as a temporary and possibly protective block in achatinids suggests that possibly the primary adaptive value of the pseudo-operculum was protection.

A similar behavioral pattern involving exposure of the left side of the body after retraction into the shell has been noted in the fresh-water basommatophoran genus *Lymnaea* (STOREY, 1972, 1983). However, this pattern was observed only as a response to drought conditions, whereas simple withdrawal during short periods of inactivity left the sole of the foot exposed in the aperture. Storey was able to demonstrate a marked reduction in the rate of water loss from the exposed body wall when compared with the foot surface in retracted snails.

Rhytidopsis (diameter 6–8 mm) is much smaller than *Pararhytida* (diameter 14–37 mm). We assume that both are descended from an even smaller ancestor that was terrestrial in habitat. Evolution of the pseudo-operculum in the ancestor would have preceded both the arboreal shift by *Rhytidopsis* and the large size by *Pararhytida*. We view this evolution as a possible release mechanism for both changes.

Large size permits *Pararhytida* to fill the size gap for a herbivorous land snail between the typical small (2–4 mm) charopids and the huge New Caledonian *Placostylus* (some over 100 mm) of the family Bulimulidae. In other faunas, this size range is filled normally by members of the Camaenidae-Bradybaenidae-Helminthoglyptidae-Helicidae lineages. These taxa have much more complex kidney and ureteric structures (BOUILLON, 1960:fig. A) than are found in the Charopidae (Tillier, unpublished data). A normal

charopid, with its simple kidney and ureter, might not find wet enough niches in New Caledonia to reach large size. With the pseudo-operculum, and in the absence of competitive snail taxa, evolution of large size and exploitation of this size range became possible.

If these views are correct, it is clear that the pseudo-operculum that evolved under predator pressure has a selective value for size increase. In this sense, the pseudo-operculum is clearly an exaptation in the sense of GOULD & VRBA (1982:4): "features that now enhance fitness but were not built by natural selection for their current role."

The above speculations go well beyond available data, but it will be many years before systematic revisions of the New Caledonian land snail taxa are completed, permitting more accurate analysis of the ecological roles played by the constituent families. Adequate comparative data for the Australian, Melanesian, and New Zealand faunas also are lacking. But perhaps presentation of these ideas will help stimulate the work needed to test them.

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Lysinoe (Gastropoda: Pulmonata) and Other Land Snails from Eocene-Oligocene of Trans-Pecos Texas, and Their Paleoclimatic Significance

by

BARRY ROTH

Museum of Paleontology, University of California,
Berkeley, California 94720

Abstract. A large helminthoglyptid land snail, *Lysinoe breedlovei* spec. nov., occurs in the Colmena Tuff and Chambers Tuff of the Vieja Group, Presidio County, Texas, associated with vertebrates of the Candelaria and Porvenir local faunas respectively. *Lysinoe breedlovei* is also present in correlative strata in the Agua Fria-Buck Hill area of Brewster County, Texas, and in a predominantly marine sequence in Nuevo León, Mexico, associated with a "Vicksburg" molluscan fauna. Associated vertebrate assemblages from the Texan localities have been assigned to the Uintan and Chadronian North American Land Mammal "Ages." Radioisotopic dates indicate a time span of about 41-38 Ma before present. The species is strikingly similar to the Holocene *Lysinoe ghiesbreghtii* (Nyst) from southern Mexico and Central America. Climatic and ecological parameters from the range of *L. ghiesbreghtii* imply that conditions in this part of Texas during the late Eocene-early Oligocene were moist and temperate and that the prevailing vegetation was probably an ecological analogue of the seasonal temperate forests of present-day Chiapas, Mexico. Mean annual rainfall in excess of 123 cm, either with or without a winter dry season, is indicated. Many plant species of the temperate Mexican forests have similar or identical counterparts in the southeastern United States. *Lysinoe* supports the concept of a formerly continuous forest distribution around the northwestern Gulf of Mexico.

The Candelaria local fauna also includes the helminthoglyptid genus *Polymita*, now confined to Oriente Province, Cuba. Other land snails from the Chambers Tuff include two subgenera of *Pleurodonte* (Camaenidae), now confined to Jamaica and the Lesser Antilles, and *Xerarionta* (Helminthoglyptidae), now living from southern California to southern Baja California. *Polymita* and *Pleurodonte* both now inhabit more tropical forests than *Lysinoe*. *Xerarionta* inhabits arid and semiarid zones within the influence of Pacific fog. By analogy with plant communities, climatic equability may have permitted the co-occurrence of genera that now show conflicting climatic preferences. The snail assemblages document a general southward retreat of land mollusk genera through the Tertiary and a developing allopatry.

INTRODUCTION

THE VIEJA GROUP of Trans-Pecos Texas and adjacent Chihuahua, Mexico, consists of about 800 m of interbedded sedimentary, volcanic, and volcanoclastic rocks of Eocene and Oligocene age. The vertebrate fossils are well studied, particularly in the so-called Rim Rock Country lying between the Rio Grande and the Sierra Vieja of Presidio and Jeff Davis counties. This area is paleontologically important because a number of radiometric dates have been obtained, in either association or superposition

with described vertebrate faunas (EVERNDEN *et al.*, 1964; WILSON *et al.*, 1968; WILSON, 1971, 1978). WILSON *et al.* (1968) mentioned in passing the presence of gastropods in rocks of the Vieja Group. PAMPE (1974) described and illustrated Vieja Group gastropods in his brief report, applying existing names from the literature of the Rocky Mountain and Great Plains regions. He evidently believed them all to be fresh-water forms; my identifications differ entirely from his. WILSON (1978) included gastropods (mostly unidentified) in his comprehensive Vieja Group faunal lists.

The Rim Rock Country is part of an unstable zone along the western flank of the late Paleozoic Diablo Platform which coincides with the eastern edge of the Mesozoic Chihuahuan Trough. During late Cretaceous/early Tertiary (Laramide) diastrophism the thick Cretaceous sediments of the trough were overthrust against the flank of the platform; after uplift and erosion of upper Cretaceous sedimentary rocks, late Eocene and early Oligocene eruptions covered most of the area with the volcanic rocks of the Vieja Group (WILSON *et al.*, 1968). The Vieja Group consists of nine named formations (DEFORD, 1958), from bottom to top the Jeff Conglomerate, Gill Breccia, Colmena Tuff, Buckshot Ignimbrite, Chambers Tuff, Bracks Rhyolite, Capote Mountain Tuff, Brite Ignimbrite (now considered part of the widespread Mitchell Mesa Rhyolite), and Petan Basalt. The rocks subsequently have been block faulted, following the general trend of the Basin and Range faulting of the late Tertiary, and carved by erosion to create a modern topography of steplike mountain slopes with extrusive rocks capping prominent ridgcrests.

On the north the Vieja Group interfingers with the Garren Group in the Van Horn Mountains. A tuff of the Garren Group in the Indio Mountains in southeastern Hudspeth County has yielded land snail fossils identified as the genus *Humboldtiana* Ihering, 1892 (UNDERWOOD & WILSON, 1974). Species of *Humboldtiana* today live in the mountains bordering the Mexican Plateau and the mountains of the Big Bend region of Texas (BURCH & THOMPSON, 1957; BEQUAERT & MILLER, 1973).

Well-preserved land gastropod fossils from the Colmena Tuff and Chambers Tuff, collected by John Andrew Wilson and parties from the University of Texas, include large snails readily identifiable as belonging to the genus *Lysinoe* Adams & Adams, 1855. The only previous Tertiary fossil record of *Lysinoe* is a tentative identification by GARDNER (1945) in the Eocene of northeastern Mexico. The species, here described as new, shows remarkable similarity to the Holocene *Lysinoe ghiesbreghtii* (Nyst, 1841) of the Mexican state of Chiapas, Guatemala, Honduras, and El Salvador, and provides a basis for interpreting the paleoecology and paleoclimate of these parts of the Vieja Group.

Also present in the Colmena Tuff is a species of *Polymita* Beck, 1837, a genus confined at the present day to eastern Cuba and having no other Tertiary fossil record. The Chambers Tuff has yielded two species here assigned to *Pleurodonta* Fischer von Waldheim, 1807, a genus now confined to Jamaica and the Lesser Antilles, and a species of *Xerarionta*, similar to present-day forms from Baja California. Samples from the Devil's Graveyard Formation in the Agua Fria-Buck Hill area, Brewster County, include *Lysinoe* and a low-spined, lenticular form tentatively assigned to the Camaenidae.

The following abbreviations are used: CAS, Department of Invertebrate Zoology, California Academy of Sciences, San Francisco; Ma (Mega-annum), 10⁶ years (before present); TMM, Vertebrate Paleontology Laboratory,

Texas Memorial Museum, University of Texas, Austin; UCMP, Museum of Paleontology, University of California, Berkeley; USGS, United States Geological Survey; USNM, Division of Paleobiology, United States National Museum of Natural History, Smithsonian Institution.

Specimen numbers of TMM consist of a five-digit locality number, a hyphen, and the specimen number from that locality, *e.g.*, 40276-16. Detailed descriptions of localities are on file at the Vertebrate Paleontology Laboratory, Texas Memorial Museum, The University of Texas at Austin. Devil's Graveyard Formation and Bandera Mesa Member are manuscript names from STEVENS *et al.* (in press) and are reserved by the Geologic Names Committee, U.S. Geological Survey.

In the species descriptions, whorls are counted by the method of PILSBRY (1939, fig. B). Shell height is measured parallel to the axis of coiling; diameter is the greatest diameter perpendicular to the axis of coiling. Both measurements exclude the expanded lip of mature specimens.

SYSTEMATIC PALEONTOLOGY

Class Gastropoda

Subclass Pulmonata

Order Sigmurethra

Superfamily Helicacea

Family HELMINTHOGLYPTIDAE

Lysinoe Adams & Adams

Aglaja ALBERS, 1850:107. *Non* Renier, 1807, *non* Eschscholtz, 1825.

Lysinoe ADAMS & ADAMS, 1855:203. MARTENS, 1890-1901: 145-147. PILSBRY, 1895:191-192. ZILCH, 1960:652.

Odontura FISCHER & CROSSE, 1870:211, 242. *Non* Rambur, 1838.

Prionodontura H. FISCHER, 1899:304.

Aglaja Albers, auctt., invalid emendation.

Type-species: *Helix ghiesbreghtii* Nyst, 1841.

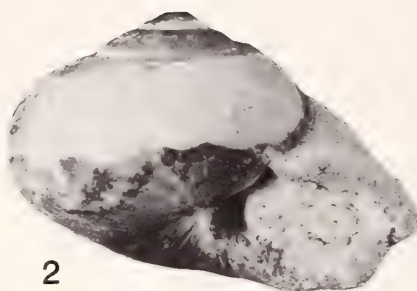
Generic diagnosis: Shell large, depressed-globose, with low spire; whorls convex, hirsute, brown with distinct banding; body whorl rounded, umbilicate; aperture oblique, lunate; lip dilated and somewhat reflected; columellar margin spread out by callus (ZILCH, 1960, translation).

The modern range of *Lysinoe* includes parts of Guatemala, Honduras, El Salvador, and the Mexican state of Chiapas. Three species are recognized: *L. ghiesbreghtii*, *L. eximia* (Pfeiffer, 1844), and *L. starretti* Thompson, 1963. The ranges of the latter two species are not well known. *Lysinoe ghiesbreghtii* is a large, conspicuous snail, gathered for food by the native peoples of Guatemala and Chiapas (MARTENS, 1890-1901; D. E. Breedlove, personal communication).

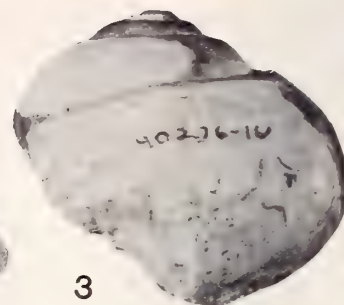
The only species originally included in *Aglaja* Albers, 1850, was *Helix ghiesbreghtii*. *Lysinoe* was proposed explicitly as a replacement name for *Aglaja* [sic] Albers, *non* Renier, and therefore takes the same type-species. A later



1



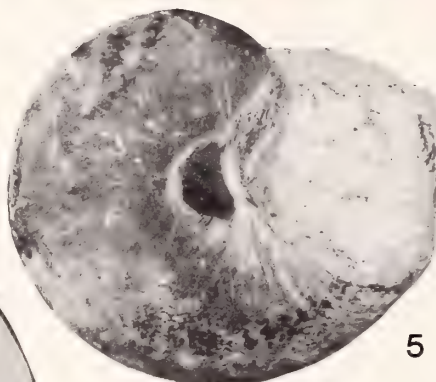
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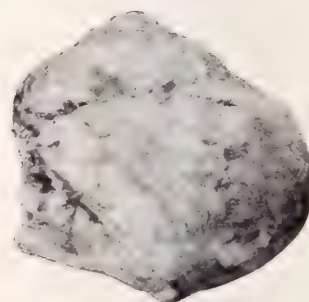
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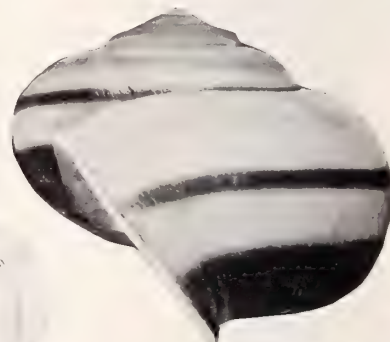
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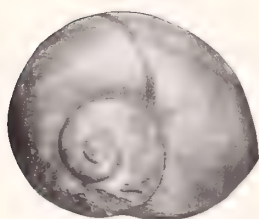
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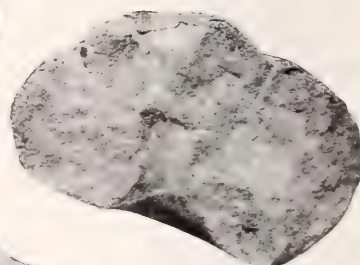
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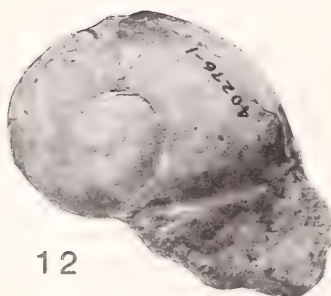
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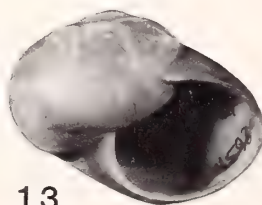
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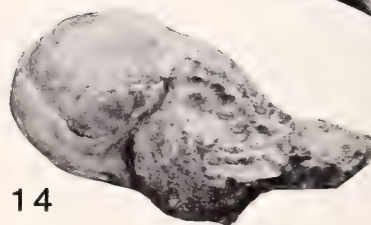
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14

designation (ALBERS, 1860) of *Helix audouinii* Orbigny, 1835, as type-species of *Aglaja* is invalid. Opinion 427 of the International Commission on Zoological Nomenclature rejected *Aglaja* [sic] Renier, 1804, for nomenclatorial purposes but reserved *Aglaja* Renier, 1807, for further consideration. *Priodontura* H. Fischer, 1899, was proposed as a replacement name for the preoccupied *Odon-tura* P. Fischer & Crosse.

Lysinoe breedlovei Roth, spec. nov.

(Figures 1–3, 5, 6, 11, 15)

"*Helix*" sp., GARDNER, 1945:18, 167; pl. 18, figs. 1–3.

[?] *Lysinoe*, GARDNER, 1945:177.

Helix leidy Hall & Meek, PAMPE, 1974:292–293 (in part), pl. 1, figs. 1–7. *Non* Hall & Meek, 1855:394.

Oreohelix grangeri Cockerell & Henderson, PAMPE, 1974: 293, pl. 2, figs. 11, 12. *Non* Cockerell & Henderson, 1912:231.

Diagnosis: *Lysinoe* with depressed-trochoid shell, about 4.75 whorls, irregular papillation, large, funicular umbilicus with circumumbilical ridge, narrowly shouldered whorls, and greatest width below middle of body whorl.

Description of holotype: Shell moderately thin, depressed-trochoid, broadly umbilicate; umbilicus funicular, contained about 6.7 times in diameter. Spire profile faintly convex; whorls of spire convex, narrowly, roundly shouldered, suture impressed. Embryonic whorls apparently about 1.5, with weak radial ribbing and a few scattered papillae, pitted by erosion. Neanic whorls with low, irregular, retractive growth rugae of varying sizes, combined on early whorls with low granulose vermiculation generally trending parallel to rugae. Rugae thickened, curved backward, and somewhat bunched below suture. From about third whorl on, also with discrete papillae, most dense on upper 1/3 of body whorl, usually irregularly spaced but in some places tending to fall in forwardly descending series. Traces of nearly obsolete spiral striation present above suture on some whorls of spire. Body whorl narrowly, roundly shouldered, widest below middle of whorl, somewhat compressed above and below periphery. Base acuminate, with distinct ridge around umbilicus. Growth rugae strong inside umbilicus; papillae sparingly

present. Last whorl slowly descending for last 1/4 turn behind lip. Aperture subquadrate, markedly oblique, at angle of 45° to axis of coiling; lip expanded and reflected. Parietal wall thickly calloused. Diameter 59.2 mm, height 40.4 mm, diameter of umbilicus 8.9 mm; whorls 4.75.

Type material: **Holotype:** TMM 40276-16; *Texas:* Presidio County: mouth of Capote Creek north of Candelaria. J. A. Wilson *et al.* coll., 28 June 1964. Colmena Tuff, Vieja Group. **Paratypes (4):** TMM 40276-18A, 40276-18B, 40276-28, 40276-29, same locality as holotype.

Referred material: TMM 31281-15 (1 specimen), 31281-20 (2), 31281-25 (1), 31281-28 (1), 31281-31 (1), 31281-35 (3), 31281-41 (1), 31281-42 (1). Presidio County: north of Capote Creek, Candelaria area. J. A. Wilson *et al.* coll., various dates between August 1960 and July 1962. Colmena Tuff.

TMM 40276-5 (1 specimen, *cf. L. breedlovei*). Presidio County: mouth of Capote Creek. J. A. Wilson coll., 7 October 1961. Colmena Tuff.

UCMP B-1362 (6 specimens, internal molds). Presidio County: 3 mi (4.8 km) north of Candelaria on north and south sides of mouth of Capote Creek; dark red-brown tuff with numerous boulder conglomerate lenses; gastropods in tuff about 70–90 ft (21–27 m) above base of Tertiary section. J. A. Wilson coll. Colmena Tuff.

TMM 41211-1 (1 specimen, figured by PAMPE, 1974, pl. 1, figs. 4, 5), 41211-2 (1). Presidio County: 0.5 mi (0.8 km) south of where road from Middleton's to Adobe Spring leaves Rooney Red Tuff Lentil. J. A. Wilson coll., 17 June 1968. Chambers Tuff, Vieja Group.

TMM 41216-5 (1 specimen). Presidio County: Capote Falls Ranch. J. A. Wilson *et al.* coll., 18 June 1968. Chambers Tuff.

TMM 41579-2 (1 specimen). Brewster County: Alamo de Cesario Creek. M. S. Stevens coll., 11 June 1973. Unnamed lower member, Devil's Graveyard Formation.

TMM 41672-22 (5 specimens). Brewster County: Purple Bench. J. A. Wilson *et al.* coll., 28 June 1974. Devil's Graveyard Formation.

TMM 41715-3 (1 specimen). Brewster County: North Fork of Alamo de Cesario Creek. M. S. Stevens coll., 18 June 1974. Skyline Channels, base of Bandera Mesa Member, Devil's Graveyard Formation.

Explanation of Figures 1 to 14

Figures 1, 2, 3, 5, 6, and 11. *Lysinoe breedlovei* spec. nov.

Figures 1, 2, 3, and 5, holotype, TMM 40276-16, top, front, lateral, and basal views; greater diameter 59.2 mm. Figure 6, referred specimen, TMM 31281-41, lateral view; diameter 41.2 mm. Figure 11, referred specimen, TMM 31281-42, cross-section; diameter 34.8 mm.

Figure 4. *Pleurodonte (Pleurodonte) wilsoni* spec. nov., referred specimen, TMM 40206-8; diameter 22.0 mm.

Figures 7, 8, and 10. *Lysinoe ghiesbreghtii* (Nyst, 1841), Holocene, near San Cristobal de las Casas, Chiapas, Mexico, CAS 045384, top, lateral, and basal views; greater diameter 61.5 mm.

Figures 9 and 13. *Polymita picta* (Born, 1780), Holocene, Mesa de Ovando, Oriente Province, Cuba, CAS 045385, top and front views; specimen coated for photographing; greater diameter 34.0 mm.

Figures 12 and 14. *Polymita texana* spec. nov., holotype, TMM 40276-1, top and front views; greater diameter 38.5 mm.

TMM 42019-19 (1 specimen). Brewster County: Red Hill, east side, same level as Balanced Rock, Coffee Cup Ranch. M. S. Stevens coll., 21 June 1977. Devil's Graveyard Formation.

TMM 42151-5 (3 specimens). Brewster County: South of Stone Corral. M. S. Stevens coll., 16 June 1977. Cotter Channels, Bandera Mesa Member, Devil's Graveyard Formation.

I have not personally examined specimen TMM 41578-3 from the "Skyline Red Ss." (=Devil's Graveyard Formation) figured by PAMPE (1974, pl. 1, figs. 1-3; as "*Helix leidy*") but from the illustration it is clearly *L. breedlovei*.

Additional description: Most of the paratype and referred material agrees in character with the holotype. A referred specimen from locality TMM 31281 shows better than the holotype the extent to which the peristome may turn outward at maturity (Figure 6). Some specimens have been compressed dorsoventrally during preservation; these show an artificially emphasized peripheral angulation. Others have been compressed or skewed laterally. Post-mortem changes aside, there seems to have been some variation in height of spire and degree of depression of the body whorl. A cross-section (Figure 11) shows that the axis is perforate throughout growth and that the circum-umbilical ridge is more acute on the early whorls.

The shell structure of *Lysinoe ghiesbreghtii* consists of (1) a thin inner lining probably of complex-prismatic structure (terminology after MACCLINTOCK, 1967); (2) a thick crossed-lamellar layer with first-order lamellae parallel to growth lines, intertonguing with (3) a second, equally thick, crossed-lamellar layer with first-order lamellae oriented at right angles to the first and parallel to the direction of growth. Fracture sections on the inner lip and body whorl of the holotype of *L. breedlovei* show that, although the shell has recrystallized, these three basic structural layers were originally present.

Referred specimen TMM 42019-19 shows a pronounced thickening and subsequent discordance of growth rugae at the 1.5-whorl stage. This appears to represent the change from embryonic to neanic shell growth.

One specimen, TMM 40276-5 (Figure 15), is exceptionally large. Although missing three quarters of the fourth whorl, the remaining internal mold is 81.2 mm in greatest diameter. The original diameter was probably in excess of 95 mm. The axis is perforate and the whorl cross-section like that of other specimens at hand. A small amount of recrystallized shell remaining around the axis shows shell layers of the same proportions as the holotype of *L. breedlovei*.

Remarks: *Lysinoe breedlovei* closely resembles the Holocene *Lysinoe ghiesbreghtii* (Nyst) (Figures 7, 8, 10) in size, general proportions, rate of augmentation of the whorls, and shape of aperture and umbilicus. The angle of obliquity of the aperture, in relation to the coiling axis,

is about 40° in *L. ghiesbreghtii*. The umbilicus of *L. breedlovei* is wider (Figure 5) and the circum-umbilical ridge of the base more pronounced. The body whorl of *L. ghiesbreghtii* is more tumid, with the widest part being near the middle, rather than below it as in *L. breedlovei*. In *L. breedlovei* the last whorl increases its rate of descent along the coiling axis slowly over the last ¼ turn (Figures 3, 6), whereas in *L. ghiesbreghtii* there is a sharp downturn about 1 cm behind the outer lip (Figure 8). *Lysinoe ghiesbreghtii* averages 5.1-5.25 whorls at maturity, slightly more than *L. breedlovei*.

The spire and upper part of the body whorl of *L. ghiesbreghtii* bear fine periostracal hairs arranged in diagonal series. Each of these is borne on a low, round, 0.1 mm-wide papilla reflected in the underlying calcareous layer of the shell. Papillae are present on the holotype of *L. breedlovei* but are not as regularly disposed.

Lysinoe breedlovei is the same species reported as "*Helix*" sp. by GARDNER (1945) from beds she assigned to the Oligocene, in Nuevo León, Mexico. Gardner herself noted the similarity to *Lysinoe*. Her figured specimen (USNM 497132) and others are internal molds with minor traces of shell remaining. They show no taxonomic characters to separate them from *L. breedlovei* of the Vieja Group. The occurrence is in a predominantly marine sequence. At one locality (USGS 14023) the species was associated with the estuarine mollusks *Erodona* and *Ampullina* and the fluviatile gastropod *Hemisinus*, indicative of permanent (not seasonal) running water. As discussed below under "Age and Correlation," the occurrence is significant for marine-nonmarine temporal correlations. The specimen from the Yegua Formation (Eocene) at Ochoa, Tamaulipas, referred to *Lysinoe* by GARDNER (1945:177) is, at this writing, temporarily unavailable for borrowing (T. R. Waller, *in litt.*, 1983) but should also be examined in this context.

The large, umbilicate land snail described as *Helix spatiosa* Meek & Hayden, 1861, from the upper Paleocene to middle or upper Eocene of the Rocky Mountain and northern Great Plains regions, discussed as the type-species of an unnamed new genus by TAYLOR (1975), differs from *L. breedlovei* in having six or more tightly coiled whorls and apical sculpture of retractive riblets like those of *Orcohelix*.

The large *Helix hesperarche* Cockerell, 1914, from an unknown locality but thought to be from the Eocene of New Mexico, differs in having the whorls more tightly coiled and the umbilicus narrower (0.12 times diameter, versus 0.15-0.16 in *L. breedlovei*). HENDERSON (1935) thought he recognized "*H.*" *hesperarche* from "the O-2 Ranch, about 25 miles south of Alpine," Texas. I have not examined Henderson's specimens, but it seems likely that he had *L. breedlovei*.

PAMPE (1974), possibly taking a cue from Russell (in GOLDICH & ELMS, 1949), referred large specimens of *L. breedlovei* to *Helix leidy* Hall & Meek, 1855, and small-

er internal molds of the same species to *Oreohelix grangeri* Cockerell & Henderson, 1912. "*Helix*" *leidyi* from the White River Group of South Dakota and Nebraska is a globose form with narrow umbilicus, not assignable to any modern genus of Helminthoglyptidae. *Oreohelix grangeri* from the lower Eocene of Bighorn Basin, Wyoming, is a depressed, carinate form that may represent young individuals of "*Helix*" *spatiosa*.

Etymology: The species is named for Dennis E. Breedlove, Curator of Botany, California Academy of Sciences, and expert on the flora of Chiapas, in recognition of his personal investigations of *Lysinoe* and other Mexican mollusks.

Polymita Beck

Polymita BECK, 1837:44. PILSBRY, 1895:187–189. TORRE Y HUERTA, 1950:7–9. MORENO, 1950:21–35. ZILCH, 1960:662.

Oligomita TORRE Y HUERTA, 1950:18.

Type-species: *Helix picta* Born, 1780.

Generic diagnosis: "Shell subglobular, brilliantly colored, rather thin but solid, imperforate; whorls few (about four), the last but little deflexed; aperture rounded, slightly lunate, the peristome simple, not expanded or reflexed except at axis, where it is reflexed and adnate over the umbilical region; axis solid" (PILSBRY, 1895:188).

The modern range of the genus is restricted to Oriente Province, eastern Cuba. The species of *Polymita* are arboreal and probably feed on epiphytic fungi and lichens (TORRE Y HUERTA, 1950).

Polymita texana Roth, spec. nov.

(Figures 12, 14)

Diagnosis: *Polymita* with large, depressed-globose shell with low spire, very rapidly enlarging body whorl, and large first nuclear whorl.

Description of holotype: Shell large for the genus, thin, depressed-globose, of 3.75 rapidly enlarging whorls; spire low; suture not deeply impressed. Embryonic whorls about 1.3, smooth, demarcated from neanic whorls by a weak constriction. Neanic whorls smooth, with almost obsolete, rounded growth lines and impressed radial growth rests at intervals of one half to one whorl. First neanic whorl with two prominent radial rugae right after embryonic whorls, and an impressed growth rest at first half whorl. Prominent growth rests occurring at 1.8, 2.8, and 3.3 whorls, with an internal thickening of the shell wall at each rest, followed by a sudden increase in internal whorl diameter. Periphery broadly rounded; body whorl descending slowly toward aperture, slightly constricted behind outer lip. Outer lip weakly turned outward, internally thickened by low smooth ridge along margin. Parietal wall simple, smooth; inner lip with thin secondary layer

of smooth callus reflected over columella. Major diameter 38.5 mm, minor diameter (incomplete) 27.2 mm, height 25.9 mm.

Type material: Holotype: TMM 40276-1. *Texas:* Presidio County; mouth of Capote Creek north of Candelaria. Bill Brannan coll., 1957. Colmena Tuff, Vieja Group.

Remarks: The rapid rate of whorl expansion of the few-whorled, subglobose shell, the steplike enlargement of whorl diameter after a growth rest, and the smooth secondary callus reflection over the columellar region are all distinctive characteristics of *Polymita*, and most similar to *Polymita picta* (Born) (Figures 9, 13).

The holotype (the only known specimen) is a nearly intact internal mold with pieces of shell remaining at the apex, on the outer part of the body whorl back for $\frac{1}{3}$ turn from the outer lip, and around the columellar margin of the aperture. It differs from *P. picta* in having 0.25–0.5 whorl less (based on large specimens of *P. picta*) and a larger first nuclear whorl—1.6 mm in diameter compared to 1.25 mm for *P. picta*. The shell has been slightly distorted in preservation, but the spire probably was lower originally than the average spire of *P. picta*. The outer lip of the fossil turns out more strongly than that of *P. picta*.

The holotype is distinguishable from *Humboldtiana* by its smooth surface, without any trace of granulose or papillose sculpture or the heavy, irregular growth wrinkles characteristic of that genus. Many species of *Humboldtiana* have nuclear whorls the same size as this fossil; most have a radially wrinkled protoconch, but this fine sculpture is readily removed by erosion even in living snails. *Humboldtiana* are narrowly umbilicate. The inner lip callus of the specimen at hand is broken at the lower end and may originally have left exposed a small umbilical chink, but the part that remains extends lower on the shell and is more broadly spread onto the body whorl than in any known *Humboldtiana* species.

Xerarionta Pilsbry

Xerarionta PILSBRY, 1913:382. PILSBRY, 1939:214–215.

Type-species: *Arionta veitchii* Tryon, 1866, ex Newcomb MS (= *Xerarionta levis canescens* [Adams & Reeve, 1848]).

Generic diagnosis: "Rather capacious, globose-conic or depressed-globose shells, perforate or closed, copiously variegated or sometimes white; the embryonic $1\frac{1}{2}$ whorls with radial sculpture or nearly smooth; peristome moderately or scarcely expanded, shortly dilated at the axial insertion" (PILSBRY, 1939:214).

Formerly considered a subgenus of *Micrarionta* Ancey, 1880, *Xerarionta* was elevated to generic rank by MILLER (1981). Its modern range includes the regions of Baja California that are influenced by Pacific Ocean fogs (MILLER, 1973; SMITH *et al.*, in preparation), the southern California Channel Islands, and the adjacent mainland.



Xerarionta areolata occurs as fossils of Pleistocene or early Holocene age on Isla Monserrate, Isla Espíritu Santo, and the nearby Baja California mainland, but there is no prior Tertiary record of the genus.

Xerarionta waltmilleri Roth, spec. nov.

(Figures 16, 17, 33)

Helix leidy Hall & Meek, PAMPE, 1974:292-293 (in part), pl. 1, figs. 8-10. *Non* HALL & MEEK, 1855:394.

[?] *Humboldtiana* UNDERWOOD & WILSON, 1974:596-597, text-fig. 2.

Diagnosis: *Xerarionta* with depressed-globose shell, umbilicus filled by impressed callus pad, tumid body whorl, and fine, even, overall granulation with granules aligning diagonally.

Description of holotype: Shell large for the genus, depressed-globose, imperforate. Spire profile slightly convex; whorls of spire flattish to weakly rounded; suture scarcely impressed until penultimate whorl. Embryonic whorls not clearly demarcated from neanic whorls. Neanic whorls sculptured with fine, even, overall granulation (best seen by low-angle light), the granules close, aligning in diagonal series; and moderately prominent, retractive growth rugae. Granulation weaker on base and perhaps also on upper part of whorl below suture; locally appearing as network of minute, diagonal, incised grooves. Body whorl tumid, moderately compressed above the well-rounded periphery. Base inflated, umbilical region not strongly indented. Last whorl slowly descending for last $\frac{1}{2}$ turn and weakly constricted just behind lip. Aperture semilunate, oblique; lip narrowly expanded, reflected at base. With impressed callus pad filling umbilical region. Parietal wall with thin, simple callousing. Diameter 25.9 mm, height 19.8 mm; whorls 5.1.

Type material: Holotype: TMM 40209-1006; *Texas:* Presidio County: Reeves Bone Bed, 96 Ranch. J. A. Wilson *et al.* coll., December 1966. Upper part of Chambers Tuff, Vieja Group. **Paratypes (17):** TMM 40209-502A, 40209-1007 through 40209-1022, same locality as holotype.

Additional description: The type lot consists of internal molds ranging from poor to moderately good preservation. The holotype retains considerable original shell. The regular granulose sculpture that suggests assignment to *Xerarionta* is preserved on the body whorl from right behind the aperture to about $\frac{1}{3}$ turn back (Figure 33) and at several places on the penult. A strongly compressed paratype also shows the same sculpture extending across the base almost to the umbilical region.

Remarks: The relatively symmetrical, globose shape of the body whorl, without sharp descent along the axis of coiling, is suggestive of *Xerarionta* and most plainly seen in *X. areolata* (Pfeiffer, 1845) (Figure 18). In *Humboldtiana* the body whorl expands at a greater rate and slopes obliquely down and away from the coiling axis. The aperture is more effuse. Granulose sculpture is present in some species of *Humboldtiana* but is of a different type: the granules tend to align along growth lines and often merge with the growth rugae. They are often irregular in size and only rarely produce anything like the fine, even, overall, diagonally trending fabric of the surface of *X. waltmilleri*.

Granulose sculpture also occurs in *Pleurodonte* (*Dentellaria*), but here also the granules are aligned primarily parallel to growth lines. The globose shape of *X. waltmilleri* and its simple, weakly deflected aperture distinguish it from *Pleurodonte* or any similar camaenid genera.

The microsculpture in *Xerarionta* is varied, from smooth with weak wrinkles of growth (*X. areolata*) to deeply cut

Explanation of Figures 15 to 33

Figure 15. *Cf. Lysinoe breedlovei* spec. nov., referred specimen, TMM 40276-5, top view; greatest diameter 81.2 mm.

Figures 16, 17, and 33. *Xerarionta waltmilleri* spec. nov., holotype, TMM 40209-1006. Figures 16 and 17, top and front views; greater diameter 25.9 mm. Figure 33, SEM photograph of diagonal microsculpture obliquely crossing growth rugae (curved horizontal ridges) on body whorl behind outer lip, $\times 20.7$.

Figure 18. *Xerarionta areolata* (Pfeiffer, 1845), Holocene, shore of Bahía Magdalena, Baja California Sur, Mexico, CAS 045386; diameter 25.6 mm.

Figures 19, 20, 23, 24, and 25. *Pleurodonte* (*Pleurodonte*) *wilsoni* spec. nov. Figures 19 and 20, holotype, TMM 40840-50, top and basal views; greater diameter 24.5 mm. Figures 23 to 25, paratype, TMM 40840-52, top, basal, and lateral views; greater diameter 24.1 mm.

Figures 21 and 22. *Pleurodonte* (*Dentellaria*)(?) species, referred

specimen, TMM 40206-56, top and basal views; greater diameter 17.7 mm.

Figure 26. *Pleurodonte* (*Pleurodonte*) *isabella* (Ferussac, 1821), Holocene, St. John's churchyard, Barbados, CAS 045388; greater diameter 23.6 mm.

Figures 27, 28. *Pleurodonte* (*Dentellaria*) *anomala* (Pfeiffer, 1848), Holocene, Jamaica, CAS 045387; greater diameter 22.3 mm.

Figures 29, 30, and 31. Camaenid, genus and species indet., referred specimen, TMM 41579-49, top, front, and basal views; greater diameter 16.1 mm.

Figure 32. *Xerarionta redimita* (Binney, 1858), Holocene, between Horse and Red Rock canyons, San Clemente Island, California, CAS 045389; SEM photograph of diagonal microsculpture on lower part of body whorl behind outer lip, $\times 22.0$. Specimens in Figures 16 to 33 have been coated for photographing.

by incised spiral grooves (*X. intercisa* [Binney, 1857], *X. pandorae* [Forbes, 1850]). The only extant species with minute overall granulation are *X. redimita* (Binney, 1858) (Figure 32) from San Clemente Island, and *X. kellettii* (Forbes, 1850) from Santa Catalina Island, California, and the adjacent mainland. The microsculpture of *X. kellettii* is often faint or reduced to minute diagonal grooves between growth lines, especially on the base. A small amount of granulation can sometimes be seen on the first neanic whorl of *X. areolata*; no diagonal trend is evident. *Xerarionta levis* (Pfeiffer, 1845) has granulose wrinkling upon the first and second neanic whorls, much more irregular than that of *X. redimita* and *X. kellettii*.

Xerarionta waltmilleri may be the same species reported as *Humboldtiana* from the Garren Group, Hudspeth County (UNDERWOOD & WILSON, 1974). As of this writing, those specimens are temporarily unavailable for borrowing (T. R. Waller, *in litt.*, 1983) but should be re-examined later.

Etymology: The species is named for Walter B. Miller of the University of Arizona, in recognition of his many contributions on the Helminthoglyptidae and other mollusks of the American Southwest.

Superfamily CAMAENACEA

Family CAMAENIDAE

BISHOP (1979) summarized the Tertiary species from North America that have been assigned to the Camaenidae. A species of *Caraculus* Montfort, 1810, *C. aquilonaris* Bishop, 1979, has been recognized in the upper Oligocene Whitney Member of the Brule Formation, White River Group, Sheridan County, Nebraska. SOLEM (1978) commented on the similarity between *Hodopoeus crassus* Pilsbry & Cockerell, 1945 (described from an unknown locality but thought to be from the Eocene of the southwestern United States), and several species of *Iso-meria* Albers, 1850. COCKERELL (1914) suggested a relationship between his *Helix hesperarche* and West Indian Camaenidae; the holotype, an internal mold, lacks the apertural characters that could confirm this placement.

Pleurodonte Fischer von Waldheim

Pleurodonte FISCHER VON WALDHEIM, 1807:229. WURTZ, 1955:119–120. ZILCH, 1960:601.

Type-species: *Helix lychnuchus* Müller, 1774.

Subgenus *Pleurodonte*, *sensu stricto*

Subgeneric diagnosis: Shell solid, globose or depressed, with low, convex, conical spire; body whorl rounded or angulate, imperforate; aperture oblique, broader than high; lip dilated and strongly thickened, mostly toothed, the limbs connected by a more or less robust parietal callus, which sometimes is also toothed (ZILCH, 1960, translation).

The modern range of *Pleurodonte*, *sensu stricto* is limited to the Lesser Antilles. One or more other species occur in

the Miocene of Carriacou, Grenadines (JUNG, 1971). *Pleurodontites* Pilsbry, 1939, from the Tampa Limestone (lower Miocene) is probably closely related. "*Pleurodonte*" *eohippina* Cockerell, 1915, from the Sand Coulee Beds, Eocene (Wasatchian), Clarks Fork Basin, Wyoming, was regarded as a helicid prosobranch and made the type-species of a new genus, *Eohiptychia*, by BISHOP (1980), but the available information on the unique specimen is not adequate to permit critical commentary on its ordinal placement (SOLEM, *in press*).

BISHOP (1979) suggested that antecedents to *Pleurodonte* were once widespread throughout the Antilles but that *Pleurodonte* has become extinct on Cuba, Hispaniola, and Puerto Rico. The new species next described and the following one show that *Pleurodonte* was already differentiated in North America by the late Eocene and that at least two types of shell form were present at that time.

Pleurodonte (*Pleurodonte*) *wilsoni* Roth, spec. nov.

(Figures 4, 19, 20, 23–25)

Polygyra veterniior (Cockerell), PAMPE, 1974:293–294 (*in part*), pl. 2, figs. 5–7. *Non Helix veterna veterniior* COCKERELL, 1915:117.

Diagnosis: *Pleurodonte* with depressed, tumid, imperforate shell, 4.7–5.1 whorls, periphery rounded to angular, body whorl sharply deflected downward behind aperture, lip thickened but not dentate.

Description: Shell small for the subgenus, depressed, imperforate. Spire low, obtuse; spire profile convex; suture lightly impressed, more deeply incised around last 0.5–0.75 whorl. Embryonic whorls not well differentiated from neanic whorls. Surface apparently smooth, with blunt, indistinct growth rugae. Body whorl narrow, with rounded or subangular periphery; base compressed, smooth, flattish. Last whorl turning sharply downward behind aperture. Aperture broadly crescentic, very oblique, at angle of 60–70° to axis of coiling; lip expanded and strongly thickened but not dentate; parietal wall callused, without teeth. Diameter of holotype 24.5 mm, height 14.2 mm; whorls 4.8.

Type material: **Holotype:** TMM 40840-50; *Texas:* Presidio County: Chalk Gap Draw. J. A. Wilson coll., June 1965. Upper part of Chambers Tuff, Vieja Group. **Paratypes (8):** TMM 40840-52 (1), 40840-53 (7), same locality as holotype.

Referred material: TMM 40206-8 (1 specimen), 40206-54 (1), 40206-55 (1). Presidio County: Northwest of Big Cliff. J. A. Wilson coll., 19 June 1960. Lower part of Chambers Tuff.

TMM 40209-502 (4 specimens; one figured by PAMPE, 1974, pl. 2, figs. 5–7, as "*Polygyra veterniior*"; associated with Little Egypt local fauna, not Candelaria local fauna as stated). Presidio County: Reeves Bone Bed, 96 Ranch.

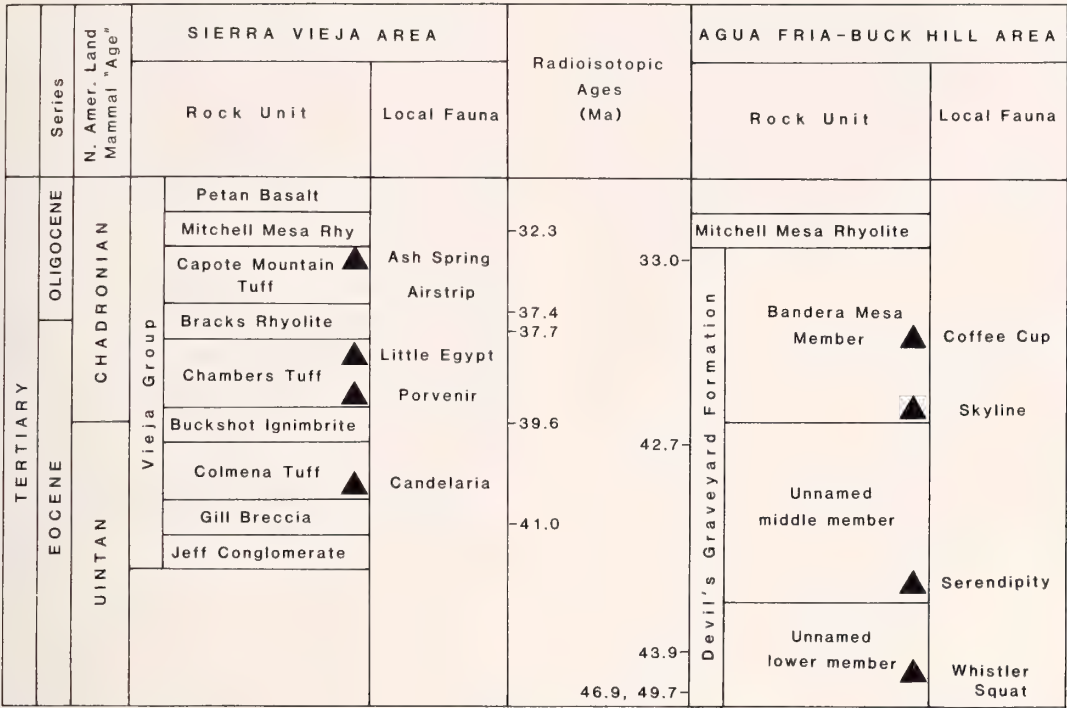


Figure 34

Correlation of rock units, radioisotopic ages, and mammal-based local faunas in Sierra Vieja and Agua Fria-Buck Hill areas. Filled triangles indicate sources of land mollusks reported in this study. Radioisotopic ages from WILSON *et al.* (1968) and WILSON (1978, and personal communication, 1983), corrected for new decay and abundance constants (DALRYMPLE, 1979).

J. A. Wilson *et al.* coll., 1966. Upper part of Chambers Tuff.

TMM 40283-82 (10 specimens). Jeff Davis County: Ash Spring. J. A. Wilson coll., 16 June 1965. Vieja Group, undifferentiated.

Additional description: The description given above is composite, because no single specimen in the type lot shows all the characters. All specimens are internal molds, with scraps of recrystallized shell remaining, mainly in the suture but occasionally around the aperture or on the spire. The major variation is in the shape of the periphery, which ranges from evenly rounded to subangular in the type lot. The referred material from the Big Cliff locality (TMM 40206) is lenticular (Figure 4) with a distinctly angled periphery. Material from the undifferentiated Vieja Group at Ash Spring is rounded, with only a hint of angulation showing on some specimens. Comparable variability is known in some modern species of *Pleurodonte*, for example *P. acuta* (Lamarck) illustrated by PILSBRY (1889-1890, pl. 26). It is also possible that sedimentary compaction tends to emphasize the peripheral angulation, as in *Lysi-noe breedlovei*.

Representative "mature" specimens (those with thickened lip) measure:

Locality	Diameter	Height	No. of whorls
TMM 40840	24.1 mm	13.6 mm	4.75
	23.5	13.2	4.75
TMM 40206	21.7	12.1	5.1
TMM 40209	20.5	12.3	4.75
	19.2	12.6	5.1
TMM 40283	24.1	17.0	5.0
	23.6	13.0	4.7
	23.1	14.6	5.1
	23.0	14.5	5+
	22.8	14.2	4.9
	22.2	14.3	4.7

Several specimens show a slight upward constriction of the base of the last whorl directly behind the aperture. This is a relatively common feature in *Pleurodonte* and other genera of American Camaenidae.

Remarks: *Pleurodonte wilsoni* resembles the Holocene *Pleurodonte isabella* (Ferussac, 1821) (Figure 26) and several other related species. The group was most comprehensively reviewed, at least for shell characters, by PILSBRY (1889-1890, 1893-1895). The spire of *P. isabella* is more domelike and the suture scarcely impressed at all until the last whorl. An irregular or denticulate ridge runs along

the basal lip of *P. isabella*; there is evidently no such ridge in *P. wilsoni*. *Pleurodonte lehneri* (Trechmann, 1935) from the Miocene of Carriacou, Grenadines, is also similar but has a strong, prominent tooth in the middle of the upper lip and two sometimes poorly developed denticles on the basal lip. Its spire is often, although not invariably, higher, and more domelike. Most specimens are less than 20 mm in diameter. However, the holotype of "*Helix*" *carriacouensis* (Trechmann, 1935), synonymized with *P. lehneri* by JUNG (1971), is 24.6 mm wide.

Helix veterna veternior Cockerell, 1915, from the lower Eocene of Wyoming, is a more globose form, apparently known from immature specimens only. It does not have the oblique aperture, descending last whorl, upwardly constricted base, or any other characters that would permit it to be associated with *P. wilsoni*.

Etymology: The species is named for John Andrew Wilson, who has contributed more than anyone else to the knowledge of Vieja Group paleontology.

Subgenus *Dentellaria* Schumacher

Dentellaria SCHUMACHER, 1817:69, 230. WURTZ, 1955:125–128. ZILCH, 1960:602.

Lucerna "Humphrey" SWAINSON, 1840:328. *Non* Willoughby, 1816.

Type-species: *Helix sinuata* Müller, 1774.

Subgeneric diagnosis: Shell solid, depressed-globose to lenticular; 4.5–6 whorls, finely and densely granulose; body whorl rounded or carinate, descending toward the aperture, umbilicate or imperforate; aperture very oblique, broader than high; lip broadly reflected; basal lip with 0–5 teeth, the limbs connected by a toothless parietal callus (ZILCH, 1960, translation).

WURTZ (1955) found the anatomical differences between *Dentellaria* and *Pleurodonte*, *sensu stricto* to be minor and kept the two taxa separate (as infrasubgeneric "sections") solely on conchological grounds.

The modern range of *Dentellaria* is limited to Jamaica. Two species occur at Bowden, Jamaica, in beds assigned a Pliocene age (BISHOP, 1979). SOLEM (1978) assigned *Kanabohelix kanabensis* (White, 1876), from the upper Cretaceous of Utah, to the Camaenidae; he remarked on its similarities to *Dentellaria*, but kept the two genera separate. BISHOP (1980) considered *K. kanabensis* a helicininid prosobranch on the basis of the form of its palatal barriers; but because it retains internal whorl partitions, SOLEM (in press) restored it to the Camaenidae.

Pleurodonte (*Dentellaria*)(?) species

(Figures 21, 22)

Description: Shell depressed, broadly umbilicate, with 3.8 whorls preserved at a diameter of 17.7 mm; nearly flat-spined, with first whorl apparently depressed slightly below level of second; suture distinct, shell wall thickened on either side. Periphery rounded, widest above middle;

last preserved whorl narrow, cross-section taller than broad; base narrowed, with acuminate circum-umbilical ridge; umbilicus large, steep-sided. Apertural characters not preserved (specimen immature).

Referred material: TMM 40206-56 (1 specimen). *Texas*: Presidio County: Northwest of Big Cliff. J. A. Wilson *et al.* coll., 19 June 1960. Lower part of Chambers Tuff, Vieja Group.

Remarks: The single specimen at hand is an internal mold with traces of thoroughly recrystallized shell remaining at the suture, on the parietal wall, and around the umbilicus. Although the specimen is obviously immature and shows none of the characters of an adult peristome, it is similar to the Jamaican *Pleurodonte* (*Dentellaria*) *anomala* (Pfeiffer, 1848) (Figures 27, 28). The almost flat spire with depressed first whorl and the narrow whorl cross-section are similar in both. At the level of the suture, the shell of *P. anomala* is thickened by a small spiral carina to which the summit of the subsequent whorl is appressed. The shell of the fossil is thickened (although not carinate) at the same position, and the shell remaining outboard of the suture is also quite thick. *Pleurodonte anomala* has even, overall granulation. The only section of shell on the fossil not too recrystallized to show the original surface is around the umbilicus inside the last whorl; this is smooth with faintly raised growth lines. The umbilicus is more steeply walled and the base more acuminate than in *P. anomala*.

Camaenid, genus and species indet.

(Figures 29–31)

Polygyra veternior (Cockerell), PAMPE, 1974:293–294 (in part), pl. 2, figs. 8–10. *Non Helix veterna veternior* COCKERELL, 1915:117.

Description: Shell lenticular, umbilicate, of 5.1 whorls. Spire low, whorls little inflated; suture moderately impressed, distinct. Embryonic whorls not well differentiated from neanic whorls. Whorls narrowly, obtusely shouldered; periphery rounded-subangulate, widest part above middle of penult but descending below middle on body whorl. Preserved sculpture of a few low, irregular, forwardly bowed, retractive growth rugae. Body whorl with flat shoulder, not markedly descending until 0.1 whorl behind aperture, where it turns down at angle of about 30° from horizontal. Base compressed, constricted upward behind aperture; umbilicus 0.14 times diameter. Aperture broadly ovate, very oblique, at angle of 60–70° to axis of coiling; lip simple, turned outward but little thickened, encroaching on umbilicus but not appressed at base. Parietal wall with thick wash of callus but no denticulation. Diameter 16.1 mm, height 8.8 mm, diameter of umbilicus 2.4 mm.

Referred material: TMM 41579-49 (1 specimen). *Texas*: Brewster County: Alamo de Cesario Creek. M. S. Ste-

vens coll., 11 June 1973. Unnamed lower member, Devil's Graveyard Formation.

Remarks: The single specimen consists of thoroughly recrystallized shell around a light, yellowish-gray, tuffaceous siltstone matrix. Although quite well preserved, it cannot be assigned to any known genus. The lenticular shape and umbilicate base suggest *Oreohelix* Pilsbry, 1904 (*Oreohelicidae*) but the outward-turning lip and the sharp terminal downward deflection of the body whorl are not typically oreohelicid. In contrast, the slight upward constriction of the base behind the aperture is a feature seen in several American genera of the Camaenidae. A constriction of about the same relative magnitude occurs in several species of *Isomeria* Albers, 1850. Almost all living species of *Isomeria* are large-shelled (to a diameter of 70+ mm). The only one normally under 20 mm when adult is *I. minuta* Solem, 1966. Several species of *Labyrinthus* Beck, 1837, become adult in the 15–20 mm diameter size range, although most are larger (to 60 mm). In all modern species the basal constriction is pronounced and the aperture provided with various denticles and lamellae.

The specimen was taken with numerous specimens of a planorbid fresh-water gastropod discussed and illustrated by PAMPE (1974, pl. 2, figs. 1–4) under the name *Biomphalaria spectabilis* (Meek).

AGE AND CORRELATION

The type locality of *Lysinoe breedlovei*, at the mouth of Capote Creek on the Rio Grande about 2 mi (3.2 km) north of Candelaria, is the source of the Candelaria local fauna. This fauna, summarized by WILSON (1978, tables 1, 2, 14) is assigned to the Uintan North American Land Mammal "Age" (BLACK & DAWSON, 1966; WILSON *et al.*, 1968; WILSON, 1978) (Figure 34). From a study of the rodents, WOOD (1974) suggested that the Candelaria local fauna was slightly younger than the Myton local fauna of the Uinta Formation of Utah.

The Colmena Tuff is bracketed stratigraphically by radioisotopic dates based on potassium-argon analysis of sanidine concentrates. Volcanic rock from the Gill Breccia, underlying the Colmena Tuff, yielded an age determination of 40.0 ± 2.0 Ma (WILSON *et al.*, 1968, figs. 1, 2, table 3; sample "0"). Corrected for the new ^{40}K decay and abundance constants (DALRYMPLE, 1979) the determination is equivalent to 41 ± 2 Ma. Three samples from the Buckshot Ignimbrite, which overlies the Colmena Tuff, yielded age determinations of 35.2 ± 2.3 Ma, 34.7 ± 2.0 Ma, and 38.6 ± 1.2 Ma (WILSON *et al.*, *loc. cit.*; samples 1, 2, and 2a respectively). The latter two determinations were made from the same rock specimen; the authors give reasons for favoring the older age determination. Corrected for the new constants it sets a minimum age of around 39 Ma for the Candelaria local fauna.

In the lower part of the Chambers Tuff, *Lysinoe breedlovei*, *Pleurodonte wilsoni*, and *Pleurodonte (Dentellaria)*(?) sp. are associated with the Porvenir local fauna.

This fauna, summarized by WILSON (1978, tables 3–7, 14) is assigned to the early part of the Chadronian North American Land Mammal "Age" (WILSON *et al.*, 1968; WILSON, 1978). The fossil localities lie stratigraphically above the Buckshot Ignimbrite with its K-Ar ages as given above, and below the Bracks Rhyolite, which has yielded age determinations of 36.8 Ma (EVERNDEN *et al.*, 1964) and 36.5 ± 1.2 Ma (WILSON *et al.*, 1968). Corrected for the new constants, these determinations are equivalent to 37.7 and 37.4 ± 1.2 Ma.

Pleurodonte wilsoni and *Xerarionta waltmilleri* occur in the upper part of the Chambers Tuff, associated with the Little Egypt local fauna. This fauna, summarized by WILSON (1978, tables 8–10, 14) is also Chadronian (WILSON *et al.*, 1968; WILSON, 1978). The Bracks Rhyolite is absent in the areas where the Little Egypt local fauna occurs (Chalk Gap Draw and the Reeves Bone Bed), but a red sandstone that elsewhere lies immediately under the Bracks is present. The age of this fauna is therefore regarded as constrained by the same radioisotopic dates as the stratigraphically lower Porvenir local fauna.

Pleurodonte wilsoni also occurs in the undifferentiated Vieja Group at the Ash Spring locality in Jeff Davis County (loc. TMM 40283), associated with the Ash Spring local fauna. This fauna is summarized by WILSON (1978, tables 12, 14). It is regarded as Chadronian, and younger than the other local faunas of the Vieja Group based on evolutionary position of vertebrate taxa (WILSON, 1978: 27).

Correlation of units in the Agua Fria–Buck Hill area (Figure 34) is based on unpublished information supplied by J. A. Wilson (personal communication, 1983). *Lysinoe breedlovei* occurs in association with the Whistler Squat (early Uintan), Serendipity (late Uintan), Skyline, and Coffee Cup (early Chadronian) local faunas. Radioisotopic ages (corrected) of 32.3 Ma from the Mitchell Mesa Rhyolite, which overlies the Devil's Graveyard Formation, and 33.0 Ma from basalt high in the Bandera Mesa Member of the Devil's Graveyard Formation set a minimum age for the Coffee Cup local fauna. An isotopic age of 42.7 Ma from tuff in the unnamed middle member sets a maximum age for the Coffee Cup and Skyline local faunas and a minimum age for the Serendipity local fauna. Age determinations of 43.9 Ma from biotite and 46.9 and 49.7 Ma from tuff in the unnamed lower member set a maximum age for the Serendipity local fauna and bracket the Whistler Squat local fauna.

The Decade of North American Geology (DNAG) geologic time scale (PALMER, 1983) places the Eocene–Oligocene boundary at 36.6 Ma; dates between 36.6 and 40.0 Ma are classified as late Eocene. In most of the literature on Vieja Group paleontology, however, the lower limit of the Chadronian "age" and the base of the Oligocene are treated as approximately coincident (*cf.* WILSON, 1978, fig. 5). In Figure 34 the DNAG placement of the Eocene–Oligocene boundary is followed; the boundary falls at or

slightly above the stratigraphic level of the Bracks Rhyolite. Magnetostratigraphy of the Vieja Group is in agreement with these correlations (PROTHERO *et al.*, 1982).

A number of North American land mollusks are known from deposits regarded as correlative with the Colmena Tuff or the Chambers Tuff, but only a few of the occurrences have been critically analyzed. The lower part of the Sespe Formation, Ventura County, California, is of Uintan (late Eocene) age (LILLEGRAVEN, 1979) and is the source of *Helminthoglypta? stocki* Hanna, 1934. This large land snail is definitely not a *Helminthoglypta*, but its proper allocation and paleoclimatic implications are not yet known. D. W. TAYLOR (1975, and in ROSS, 1959 [1960]) reported three species of land snails of probable late Eocene age and three others of probable Oligocene age from the Flathead River valley, Montana-British Columbia. Early Tertiary formations of the Bozeman Group in the Three Forks Quadrangle, southwestern Montana, have yielded a diverse molluscan fauna consisting of the genera *Gastrocopta* (four species), *Pupoides* (*Ischnopupoides*) (two species), *Radiocentrum* (two species), *Polygyrella*, and *Helminthoglypta* (ROTH, in press). The formations range in age from probable middle or late Eocene (Uintan or earlier) to early Oligocene (Chadronian). The assemblages have a temperate aspect and suggest that a thermal stratification—latitudinal, altitudinal, or both—existed during this time. The temporal correlations, however, are mostly inferential. TAYLOR (1975, tables 18, 27, 28, 31–33, figure 3) reported land mollusks of late Eocene to Oligocene age from formations in central, southwestern, and northwestern Wyoming. The full description of these terrestrial mollusk faunas, their interrelationships, and time correlation, remain for the future. For the present it may be noted that the molluscan faunas of the northern Cordillera have little in common with those of the Vieja Group.

Based on faunal correlation with the Chambers Tuff, UNDERWOOD & WILSON (1974) assigned an age between 38 and 39 Ma to the tuff of the Garren Group in Hudspeth County, Texas, that yielded specimens of *Humboldtiana*. Vertebrate remains from the same rock sequence correlate with the Porvenir local fauna (early Chadronian) (WILSON, 1978).

The *Lysinoe breedlovei* from Nuevo León occur low in the upper of two marine sandstones containing a "Vicksburg" molluscan fauna (GARDNER, 1945). The Vicksburg Group of the Gulf Coastal Plain traditionally has been regarded as Oligocene and correlated with the Rupelian Stage of Europe (COOKE *et al.*, 1943; BERGGREN, 1971). On the recent DNAG geologic time scale (PALMER, 1983), the Rupelian Stage is entirely post-Eocene in age, younger than 36.6 Ma. The *Lysinoe* occur with *Ampullina mississippiensis* (Conrad), which is characteristic of the Mint Spring Formation of the Vicksburg Group in Mississippi and, according to Gardner, may be restricted to that horizon. A recent faunistic study (DOCKERY, 1982) adds no new information on Mint Spring interregional correlations.

PALEOECOLOGY AND PALEOCLIMATE

Compared to that of mammals, the average rate of evolutionary change expressed in the morphology of land snails is slow. The earliest fossil land snails, from the Pennsylvanian and Permian periods, are assignable to extant families (SOLEM & YOCHELSON, 1979). Many modern genera make their first appearance in upper Cretaceous or Paleogene strata of North America, and in some cases the shells present essentially no tangible differences from those of species living today (ROTH, in press). If a low rate of change is assumed to extend to physiological tolerances as well—that is, if morphologic change is regarded as a fair sample of total evolutionary change—land snail fossils can be viewed with confidence as indicators of ancient environments.

At present the Rim Rock Country is part of the most arid region of Texas, with normal annual precipitation between 20 and 30 cm, most of it falling in summer. The mean annual temperature is 16.9°C, and there is a mean annual range of temperature of 19.5°C. The normal mean temperature for the coldest month is 7.2°C (U.S. Department of Commerce, 1968). The sparse vegetation includes cacti, yucca, sotol, lechuguilla, and ocotillo, with sagebrush and creosote bush on valley flats.

The modern distribution of *Lysinoe ghiesbreghtii* is largely within the zone of seasonal temperate forest of southern Mexico and Central America, with some extension into wet optimum forest types. The localities for which definite information is available (see Appendix) are in Pine-Oak Forest, Pine Forest (a facies of Pine-Oak Forest), Pine-Oak-*Liquidambar* Forest, and Montane Rain Forest, of BREEDLOVE's (1981) classification of vegetational formations of Chiapas. The locality "Mosquito Coast, north of Cape Gracias-à-Dios" (Honduras) by MARTENS (1890–1901) is definitely in error; his record from Hacienda Buenavista, Guatemala, at elevation 4000–5000 ft (1219–1524 m), is lower in altitude than any material I have personally examined, although the appropriate forest types extend this low (BREEDLOVE, 1981).

The Pine-Oak Forest is an open forest association composed of relatively few species of trees. Stands of pure pine or oak occur in specialized edaphic situations. The trees are commonly 15–40 m tall and variably spaced. Epiphytes are sparse to common but heavy only in canyon situations. The understory is usually herbaceous with a few shrubs (BREEDLOVE, 1981).

The Pine-Oak-*Liquidambar* Forest is a diverse plant association with many species of deciduous and semi-deciduous trees, an abundance of epiphytes, and a variable understory ranging from a dense association with many species of shrubs, subshrubs, and vines, to a tall grassy expanse with scattered shrubs. This formation is less open than Pine-Oak Forest; the trees, which may be quite broad-crowned, usually are close enough for their crowns to form a continuous canopy. This is a temperate forest quite similar to the diverse hardwood forests of the southeastern

United States, and depauperate elements of this association occur at scattered locations in the Sierra Madre of central and northern Mexico (BREEDLOVE, 1981; MIRANDA & SHARP, 1950).

Pine-Oak Forest ranges in altitude from 1300 to 2500 m with occasional patches as low as 1000 m. It exists where there is a dry season of from three to six months. Where the dry season is three months or less, it is replaced by Pine-Oak-*Liquidambar* Forest. Where a dry season is absent or at most only a few weeks in length, Pine-Oak-*Liquidambar* Forest is replaced by Montane Rain Forest or, above 2500 m elevation, by Evergreen Cloud Forest (data from BREEDLOVE, 1981, fig. 5, and personal communication). Rainfall is an important determinant of local vegetational type, as seen in the difference between east and west escarpments of the Chiapas Plateau: Pine-Oak-*Liquidambar* Forest and Montane Rain Forest cover the eastern escarpment; Pine-Oak Forest and Tropical Deciduous Forest occur on the drier west side (BREEDLOVE, 1981).

At San Cristobal de las Casas (16°44'N, 92°38'W; elev. 2755 m), typical of stations within the Pine-Oak Forest, mean annual temperature is 14.8°C and there is a mean annual range of temperature of 3.5°C. The normal mean temperature for the coldest month (December) is 12.5°C; that for the warmest months (June and July) is 15.9°C. Annual rainfall is 123 cm, 6 cm of which (less than five per cent of the annual total) falls in the period from November through February (GARCÍA, 1973). Such a climate is classified as temperate and moist, with a long cool summer (GARCÍA, 1973). Using the data of mean annual temperature and mean annual range of temperature, the nomography method (AXELROD & BAILEY, 1969) gives estimates of 197 days per year warmer than 14°C, a virtual absence of freezing temperatures, and an equability rating of 82. (Equability, as defined by Axelrod & Bailey, here means freedom from extremes of both heat and cold. A rating of 82 indicates an exceptionally equable climate.)

The rock enclosing the samples of *Lysinoe breedlovei* from the Colmena Tuff is a pinkish-brown tuffaceous siltstone, probably rhyolitic in composition, with interstitial iron oxide staining. It was undoubtedly water-laid (J. F. DeMouthe, personal communication) and suggests a humid rather than an arid climate. During deposition of the lower sedimentary facies of the Colmena Tuff, the area was apparently a broad valley occupied by meandering streams with active volcanoes not far distant (WILSON, 1978).

By analogy with *Lysinoe ghiesbreghtii*, *L. breedlovei* indicates a highly equable, moist, temperate climate, either with or without a winter dry season. The landscape was forested with vegetation like the present-day seasonal temperate forests of Chiapas (Pine-Oak or Pine-Oak-*Liquidambar*) or, possibly, Montane Rain Forest. Perhaps an analysis of the mammals of the Candelaria local fauna, when all groups have been worked up, will indicate whether a dense formation—Pine-Oak-*Liquidambar* or

Montane Rain Forest—or the relatively open Pine-Oak Forest is the more likely. There would have been a minimum of 123 cm of precipitation annually.

Lysinoe ghiesbreghtii lives at altitudes of about 1800–2700 m. The regional geology of Trans-Pecos Texas indicates that the rocks of the Vieja Group formed at lower elevations and have been raised to their present altitude (1000–2000 m) since Eocene time. The strata containing the Barrilla flora in the neighboring Davis Mountains, probably contemporaneous with the Chambers Tuff, were most likely deposited at or below 300 m altitude (AXELROD & BAILEY, 1976). Fossil floras of the Rio Grande depression, New Mexico, have undergone 1200 m of post-Eocene uplift (AXELROD & BAILEY, 1976). The specimens of *L. breedlovei* from Nuevo León were deposited in a brackish marine environment and probably transported no great distance from the interior; here also a lower elevation is indicated. Although the precipitation and thermal parameters are inferred to have been similar to those of the modern temperate Mexican forests, the topographic setting was probably much lower and in more direct communication with the coastline.

The information available on the modern habitats and environments of the other genera is much less complete or, in the case of *Xerarionta*, spans a broader range of conditions.

Locality records of *Polymita picta* (morphologically the closest species to *P. texana*) in the CAS collection indicate that the species occurs on forested terraces inland from Maisí, Oriente Province, over an altitude range of at least 180–460 m and elsewhere along the northeastern coast at least as far west as Punta Guárico. The vegetation is seasonal tropical forest with a high diversity of tree species, including *Cedrela mexicana*, *Ficus aurea*, *Ocotea leucoxydon*, *Pithecellobium saman*, *Roystonea regia*, *Spondias mombin*, and *Zanthoxylum* species (SEIFRIZ, 1943). Normal annual rainfall in the range of *P. picta* is 114–152 cm. (At Punta Maisí proper, one of the driest parts of Cuba and probably drier than the terraces inland, the annual precipitation is 78 cm [PORTIG, 1976].) For Oriente Province as a whole the driest season is December through April; in each of the months January through March there is less than 6 cm of precipitation (SEIFRIZ, 1943, fig. 6). At Punta Maisí the mean annual temperature is 26.3°C and there is a mean annual range of temperature of 4.5°C (PORTIG, 1976). The equability rating determined by nomography is 43. This is a true tropical climate with the normal mean temperature of the coldest month above 18°C. The vegetational and thermal relations are inconsistent with those based on *L. ghiesbreghtii*, although the general indications of rainfall and a winter dry season are compatible.

There is inadequate information on the total range of *Pleurodonte (Dentellaria) anomala*, the modern species similar to the *Dentellaria* of the Porvenir local fauna, but it does occur near Mandeville, Jamaica (PILSBRY & BROWN, 1910), on the bauxitic Manchester Plateau. Here the original forest has been much modified by agriculture

and grazing, but the tree species are elements of the Wet Limestone Forest, a seasonal formation (ASPREY & ROBBINS, 1953). Rainfall is between 150 and 200 cm annually with "few months" with less than 10 cm. The climate is tropical.

Pleurodonte (*Pleurodonte*) occurs in the Lesser Antilles; *P. (P.) isabella*, one of the species similar to *P. (P.) wilsoni*, lives on Barbados. At Bridgetown, Barbados, the annual rainfall is 130 cm; at Dunscombe it is 218 cm (PORTIG, 1976). March is the driest month, August the wettest. At Bridgetown the mean annual temperature is 26.3°C and there is a mean annual range of temperature of 2.0°C. The equability rating is 44. The climate is, therefore, similar to that in the range of *Polymita picta*.

Xerarionta now occurs on the southern California Channel Islands and the adjacent mainland, and along the western part of Baja California between latitudes 24–31°N. The Baja California occurrences are all within the arid, subtropical to tropical Sonoran Desert. Avalon, Santa Catalina Island (in the range of *X. kelletii*), has a mean annual temperature of 14.5°C and a mean annual range of temperature of 7.2°C, an equability rating of 72, and annual precipitation of about 33 cm (ELFORD, 1970). Representative stations within the Sonoran Desert range of the genus include El Rosario (mean annual temperature 17°C; mean annual range of temperature 10°C), Bahía Magdalena (21.5°C; 8.5°C), and Vizcaíno (19°C; 8.5°C) (AXELROD, 1979, fig. 3). Equability ratings range from 54 to 64. The nomogram indicates more than 212 days warmer than 15°C at El Rosario, more than 281 days warmer than 17°C at Bahía Magdalena. These are among the mildest and least thermally variable stations in the Sonoran Desert.

The development of the Sonoran Desert as an arid environment of regional extent was an event of latest Tertiary and Quaternary time (AXELROD, 1979). Older environments of Tropic Savanna, Dry Tropic Forest, Short-tree Forest, and drier formations contributed the ancestors of the plant taxa that now characterize the desert. While it is not justifiable to conclude that *Xerarionta waltmilleri* lived under arid conditions, on the analogy of plant history it may have been an inhabitant of relatively xeric sites in a seasonally dry tropical or subtropical forest.

From the composition of the Rancho Gaitan local fauna of northeastern Chihuahua (early Chadronian, correlated with the Little Egypt local fauna), FERRUSQUÍA (1969) inferred a woodland community, possibly with marshy habitats, and (from the presence of "thousands" of large fresh-water gastropods) the existence of a neighboring body of permanent water. Thermal parameters were not specified.

AXELROD & BAILEY (1976) interpreted a small fossil flora from the Huelster Formation in the Barrilla Mountains to represent the upper part of a dry mixed subtropical flora, analogous to modern vegetation in southern Tamaulipas and southward along the east front of the Sierra Madre Oriental. The Huelster Formation is correlated

with the Chambers Tuff (both are overlain by volcanics yielding radioisotopic ages in the 36–37 Ma range: WILSON, 1978, table 15), so climatic inferences from the Barrilla flora may also be applicable to the neighboring Chambers Tuff.

Increasing amounts of caliche cement in the sediments of the Chambers Tuff indicate that increasingly drier conditions prevailed at the time of that unit's deposition (HARRIS, 1967, M.A. thesis, Univ. Texas Austin; *vide* FERRUSQUÍA, 1969). WILSON (1978:32) also concluded that the paleoenvironment of the Chambers Tuff was "more open than that of the Colmena, more removed from direct volcanic activity and probably dryer."

In the Sierra Vieja area, *Lysinoe breedlovei* makes its last appearance in the lower part of the Chambers Tuff; its last appearance in the Agua Fria–Buck Hill area is probably not much later in time. Its local disappearance may be correlated with increasing aridity and/or decreasing equability of climate. During this interval its range may have begun to retreat southward, and possibly altitudinally upward—where the likelihood of preservation in lowland basins would be less. *Xerarionta waltmilleri* makes its first appearance in the upper part of the Chambers Tuff. The presence of this genus is consistent with drier and at least somewhat less equable conditions.

The climatic transition cannot have been too radical, however, because *Pleurodonte wilsoni* remained present throughout the interval represented by the Porvenir to Ash Spring local faunas.

The sympatry in the Vieja Group of land mollusk genera now widely separated is striking. *Polymita*, now restricted to the eastern province of Cuba, was sympatric with *Lysinoe* in western Texas during late Uintan time. Two now allopatric subgenera of *Pleurodonte* coexisted in early Chadronian time; *Lysinoe* has not yet been found at the same localities with them but comes from related sites yielding the Porvenir local fauna. *Pleurodonte* and *Xerarionta* were sympatrically associated with the Little Egypt local fauna. The history of these genera since early Tertiary time has involved both southward limitation of range and assortment into different geographic areas. How much of this change represents sorting out along environmental gradients and how much is attributable to historical accident remains a subject for investigation. At present, and presumably to a greater or lesser extent throughout the Tertiary, a southward geographic shift from North America takes a taxon into an area of smaller and more disjunct land masses, where isolation and the probability of chance extinctions are higher.

In the late Eocene paleogeographic reconstruction of the Caribbean region by SYKES *et al.* (1982, fig. 11), the various land masses now inhabited by the genera of the Vieja Group assemblage were more closely juxtaposed. The Caribbean Plate, including Central America south of the Motagua Fault, Jamaica, and the region of the Lesser Antilles, was some 1400 km farther west than at present. Jamaica is pictured as adjacent to southern Mexico, the

Lesser Antilles directly south of eastern Cuba. Somewhat earlier, 48 million years ago, Cuba was part of the East Pacific-Caribbean Plate and adjacent to the Yucatan Peninsula (SYKES *et al.*, 1982, fig. 9, top). The separation of Baja California from mainland Mexico by the rifting open of the Gulf of California is a relatively young event, perhaps beginning only four million years ago, although a proto-Gulf of California, resulting from extension behind a trench-arc system, may have existed as early as the Miocene (KARIG & JENSKY, 1972).

These paleogeographic reconstructions do not, however, eliminate the need to consider over-water dispersal in the biogeography of Caribbean land snail genera. They merely change the map on which hypothetical routes of dispersal must be plotted. For instance, depending on the (conjectural) emergence of the Nicaragua Rise, *Lysinoe* may have reached the portion of Central America on the Caribbean Plate either over water or by land in Paleogene time; or it may have made a shorter trip by land when Central America and Mexico became juxtaposed in the Miocene, between 20 and 7 Ma (SYKES *et al.*, 1982, fig. 9, center and bottom).

Sympatry of taxa now widely separated is proving to be a common phenomenon in Tertiary faunas of western North America (ROTH, in press). The same has been found true for plants (AXELROD & BAILEY, 1969:178-179):

"No Tertiary flora is duplicated exactly in any one area by modern vegetation. In part the problem [in analyzing paleoclimates] is one of species extinction, but also troublesome is the fact that living plants most similar to those of a fossil flora regularly contribute to forests that live in widely separated regions, and under different climates. For example, Miocene floras from central California to Washington are composed of plants whose nearest relatives are found in the conifer forests of the western United States, in the mixed deciduous hardwood forests of the eastern United States and in the related forests of China and Japan."

The property of equability, permitting year-long growth, and the absence of frost permit tropical plants to live together with many species found in temperate regions, as occurs in the Sierra Madre Oriental of Mexico (MIRANDA & SHARP, 1950; AXELROD & BAILEY, 1969) and in the zone of seasonal temperate forest in Chiapas. Climates of high equability were widespread in North America during the Eocene (AXELROD & BAILEY, 1969). The vegetation of the Mexican areas mentioned (including the Chiapas Plateau) includes a considerable number of species, among them the forest-dominant oaks and pines, that seem to have had a northern origin and relationships (MIRANDA & SHARP, 1950). The similarity of the Pine-Oak-*Liquidambar* Forest to the hardwood forests of the southeastern United States has already been mentioned: many plant species in eastern Mexico have very similar or identical counterparts in the eastern U.S. Miranda & Sharp regarded 16% of 200 species that occur frequently in the major temperate communities of eastern Mexico as be-

longing to this category. GRAHAM (1973) listed 21 identical species and 12 species-pairs among the arborescent (tree and shrub) genera common to the eastern U.S. and eastern Mexico. The distributions of these species and species-pairs are now disjunct (compare MIRANDA & SHARP, 1950, fig. 12), but the evidence points to a former continuity around the northwest Gulf of Mexico and for unknown distances further north and west. The finding of *Lysinoe*, a snail associated with the temperate Mexican forests, in the Eocene of western Texas, supports this scenario. However, the presence of other snail genera now inhabiting more tropical forests suggests that the forest elements may already have been somewhat mixed.

In summary, the land mollusk sequence is consistent with a transition, over late Uintan-early Chadronian time, from a highly equable, moist and temperate climate to one more arid and less equable. The beginning of the southward retreat of the ranges of several modern genera may be in evidence. Genera now allopatric were formerly sympatric. On the model of plant communities, climatic equability is probably an important factor regulating northern range limits, and perhaps generic diversity as well.

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APPENDIX:

Locality Records for *Lysinoe gheisbreghtii*

Mexico: Chiapas: Municipio Teopisca, 10 km N of Teopisca, elev. 7000 ft (2134 m), D. E. Breedlove coll., 21 Oct 1981 (CAS 029679). In hills on E side of San Cristóbal de las Casas, elev. 7400 ft (2255 m), D. E. Breedlove coll., 22 Aug 1981 (CAS 029680). Aguacutenango, elev. 5900 ft (1798 m), pine-oak forest, D. E. Breedlove coll., 12 Jun 1966 (CAS 037059). Rancho Nuevo, 8.6 mi SW of San Cristóbal de las Casas, elev. 7800 ft (2377 m), pine forest, L. Baptista coll., 19 Aug 1966 (CAS 037066). Near San Cristóbal de las Casas, elev. 7000 ft (2134 m), E. Hunn coll., 15 Nov 1971 (CAS 037065). At km 1156 on Highway 190 between Chiapa del Corzo and San Cristóbal de las Casas, elev. 7750 ft (2362 m), pine-oak forest, L. Baptista coll., 18 Aug 1966 (CAS 037062). Seventeen kilometers SE of San Cristóbal de las Casas, pine-oak forest, elev. 2195 m, D. E. Breedlove & K. E. Lucas coll., 15 Jan 1973 (CAS 037061). Along small stream on Cerro Tres Picos, elev. 7000 ft (2134 m), D. E. Breedlove coll., 28 Mar 1973 (CAS 037060). Two to four kilometers SW of Highway 190 along road to San Lucas Zapotal, elev. 7500 ft (2286 m), D. E. Breedlove coll., 8 Sep 1974 (CAS 037064). Ten and one half miles SW of San Cristóbal de las Casas, K. E. Lucas coll., 2 Sep 1972 (CAS unnumbered). SE side of Cerro Tres Picos, montane rain forest, elev. 6000 ft (1828 m), D. E. Breedlove coll., 28 May 1972 (CAS unnumbered). E side of Cerro Bola just E of Tres Picos, elev. 6000 ft (1828 m), D. E. Breedlove coll., 4 May 1972 (CAS unnumbered). Near San Cristóbal, E. Hunn coll., 1971 (CAS unnumbered). Laguna Chamula, microwave tower between Comitán and Amatenango, elev. 8300 ft (2530 m), 20 Aug 1972 (CAS unnumbered). Zinacantán, elev. 2000 m (BEQUAERT, 1957). Environs of Chiapa (FISCHER & CROSSE, 1870–1902). Rancho Nuevo, 8 mi from Las Casas (BEQUAERT, 1957). Mountain above the Sumidero near Las Casas (BEQUAERT, 1957).

Guatemala: Mountains of Alta Vera Paz (FISCHER & CROSSE, 1870–1902). Cobán (FISCHER & CROSSE, 1870–1902; MARTENS, 1890–1901). Purula, towards the head of the Polochic valley (MARTENS, 1890–1901). Cerro Zunil, on the Pacific slope, near

Quetzaltenango (*ibid.*). Hacienda Buenavista in Upper Cholutz, elev. 4000–5000 ft (1219–1524 m), in forests (*ibid.*). Depto. Solola, Toliman, in the hills above San Lucas, near the lake of Atitlán, temperate zone (FISCHER & CROSSE, 1870–1902;

MARTENS, 1890–1901). Duená (FISCHER & CROSSE, 1870–1902).

Honduras: Cordillera of San Marcos, elev. about 2660 m (FISCHER & CROSSE, 1870–1902; MARTENS, 1890–1901).

El Salvador: Volcan de Santa Ana (BEQUAERT, 1957).

The Genera *Moelleria* Jeffreys, 1865, and
Spiromoelleria gen. nov. in the North Pacific, with
Description of a New Species of *Spiromoelleria*
(Gastropoda: Turbinidae)

by

RAE BAXTER

Box 96, Bethel, Alaska 99559

AND

JAMES H. McLEAN

Los Angeles County Museum of Natural History,
Los Angeles, California 90007

Abstract. Two genera of minute turbinid gastropods in the subfamily Homalopomatinae, *Moelleria* Jeffreys, 1865, and *Spiromoelleria* gen. nov., are here called the *Moelleria* group. These genera differ from other homalopomatine genera in having a calcareous operculum with a multispiral pattern on its exterior surface, having the operculum unable to retract deeper than flush with the apertural margin, and lacking the apertural denticle of *Homalopoma* and related genera. *Moelleria* is monotypic for *M. costulata* (Möller, 1842), which has a circumboreal, offshore distribution. It has coalescing axial sculpture of a kind unknown in other living trochacean genera. Spiral sculpture is characteristic of only two shallow-water North Pacific species in the new genus *Spiromoelleria*: *S. quadrae* (Dall, 1897), the type species, and *S. kachemakensis* spec. nov. *Moelleria drusiana* Dall, 1919, is synonymized with *S. quadrae*. The three species are sympatric in the Gulf of Alaska.

INTRODUCTION

TWO SPECIES until now assigned to *Moelleria* Jeffreys, 1865, have major differences in sculpture, although these differences have not previously been thought to merit generic distinction. The discovery of a third, new species, conforming to one of the sculptural types, indicates that the two basic kinds of sculpture should be distinguished at the generic level. We, therefore, propose the new genus *Spiromoelleria*, which now includes two species; *Moelleria* remains monotypic.

The two genera differ in shell and opercular characters from genera related to *Homalopoma* Carpenter, 1864, at a level that will be treated as a tribe in a review of trochacean classification (McLean & Hickman, in preparation). In this paper we discuss these distinctions but refer to the two genera as the *Moelleria* group. The new genus

and species have already been included in a checklist of the mollusks of Alaska (BAXTER, 1983); they are first validated here.

Collections examined include those of Rae Baxter (RB), the University of Alaska, Fairbanks (UAF), the California Academy of Sciences, San Francisco (CAS), the Los Angeles County Museum of Natural History (LACM), and the National Museum of Natural History, Washington, D.C. (USNM). Voucher specimens of *Moelleria costulata*, *Spiromoelleria quadrae*, and *Homalopoma lacunatum*, and paratypes of *S. kachemakensis*, have been deposited in these institutions and in the National Museum of Canada (NMC).

Shells are illustrated by macrophotography and scanning electron microscopy (SEM). Radulae of two species are illustrated with SEM. Living specimens of *S. kachemakensis* were sketched by Baxter under a dissecting mi-

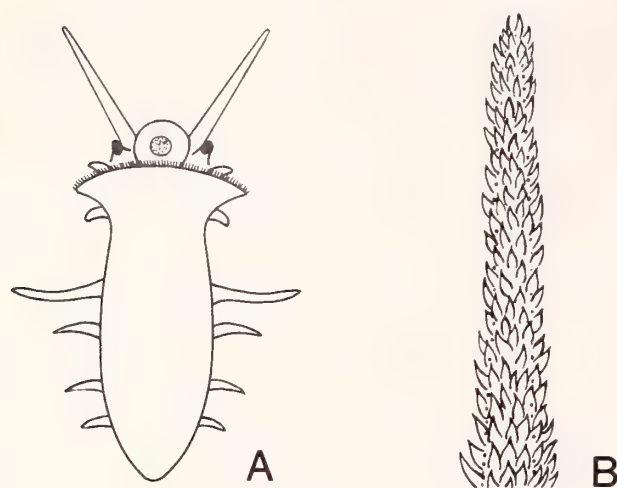


Figure 1

Spiromoelleria kachemakensis Baxter & McLean, spec. nov. Drawings of living specimen (by Baxter). A. Ventral view of head, foot, and epipodial structures, showing cephalic tentacles with eyes at base, mouth, foot (anterior tip broad with papillate edge), four pairs of epipodial tentacles, and neck lobes posterior to eyes; B. Enlarged view of cephalic (or epipodial) tentacle, showing papillae.

croscope. Shells were measured with calibration scales for a dissecting microscope.

Family TURBINIDAE

Subfamily HOMALOPOMATINAE

The *Moelleria* Group of Genera

Moelleria Jeffreys, 1865, and *Spiromoelleria* gen. nov. have the following shared features:

Shell minute (under 4 mm maximum dimension), depressed, deeply umbilicate; aperture nearly circular, only slightly oblique; columellar denticles lacking; lip not thickened. Sculpture of axial and spiral elements, or spiral elements alone. Interior nacreous layer thin. Protoconch with pointed tip, as in most trochaceans. Operculum not retractable deeper than apertural margin; interior surface of operculum flat, multispiral; exterior surface concave, also multispiral. Cephalic lappets lacking; left and right neck lobes simple; left and right epipodial ridge with four pairs of papillate epipodial tentacles; anterior end of foot with lateral tips. Rachidian tooth narrow at tip and base, broad at midpoint; lateral teeth 5, broad at midpoint and overlapping adjacent laterals; lateromarginal plate attached to base of first marginal; marginal teeth numerous, cusped.

The thin shell, thin nacreous layer, and lack of columellar denticles in the *Moelleria* group are characteristic. Genera related to *Homalopoma* Carpenter, 1864, differ in having thicker shells, a more pronounced nacreous layer, and the outer lip thickened in mature specimens.

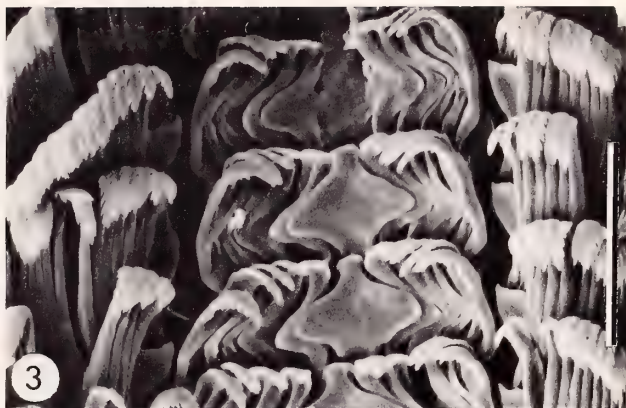
The operculum in the *Moelleria* group is multispiral on both surfaces and unable to retract deeper than flush with the apertural margin. Opercula in genera related to *Homalopoma* differ in having a paucispiral pattern on the interior surface and the exterior surface thickened by calcareous deposition close to the columellar wall, which obliterates the pattern of coiling; these opercula are capable of retracting well within the aperture.

Based on preserved specimens, FRETTER & GRAHAM (1977:93) reported for *Moelleria costulata*: "The snout is broad and depressed, the closed mouth a vertical slit at its end bordered by rather fleshy lips not split or extended mid-ventrally. The tip of the snout is not bilobed but carries a slightly scalloped edge. The tentacles are setose and are flanked laterally by eye stalks each carrying a large black eye at its tip. There are no cephalic lappets. The foot is rather straight anteriorly, its corners elongated, and tapers to a narrow posterior end. A neck lobe lies on each side, smooth-edged, unconnected to the cephalic tentacles but joined to an epipodial fold, carrying (?) 4 tentacles similar to the cephalic ones." The "setae" of Fretter & Graham are equivalent to the "papillae" of CRISP (1981), whose terminology we adopt here.

The living animal of *Spiromoelleria kachemakensis* (Figure 1) is similar to *Moelleria costulata*, as described by FRETTER & GRAHAM (1977). In dorsal view of the extended animal, only the outer portion of the cephalic tentacles and the tips of the first pair of epipodial tentacles show past the shell edge. The short foot is expanded anteriorly and bluntly pointed posteriorly; its anterior margin is finely papillate, the rest of the margin smooth. The cephalic tentacles project about 40% of shell diameter, are papillate, with the pointed, cone-shaped papillae directed anteriorly. The length of the papillae is equal to the diameter of the tentacles near their blunt tips. Along the epipodial fold there are four pairs of elongate, round, blunt-tipped epipodial tentacles, which are papillate like the cephalic tentacles. First epipodial tentacle more than twice the length of the second, the posterior the shortest; their diameter about the same as the cephalic tentacles. Eye spots are black; the eyes are on short stalks, lateral to the cephalic tentacles and are attached to them for about half their length. There are two pairs of neck lobes, which are short, smooth, and triangular in shape. The snout tip is circular, with a rounded central mouth. The operculum on the expanded animal appears to block the umbilical opening. The animal of *S. quadrae* has the posterior region of the foot with fine, short, triangulate papillae, differing from the other species in having the papillae of the tentacles much finer and more numerous.

External anatomical characters are similar to those of *Homalopoma* and related genera (McLean & Hickman, in preparation), which suggests that the *Moelleria* group should be retained in the Homalopomatinae.

Radular ribbons of four specimens of *Moelleria costulata* examined by Baxter had 35 to 44 rows of teeth and 47 to



Explanation of Figures 2 and 3

Figure 2. *Moelleria costulata* (Möller, 1842). Radular ribbon. LACM 73-23, 9 m off Hesketh Island, Kachemak Bay, Cook Inlet, Alaska. Bar = 40 μ m.

Figure 3. *Spiromoelleria quadrae* (Dall, 1897). Radular ribbon. LACM 73-22, intertidal, Yukon Island, Kachemak Bay, Cook Inlet, Alaska. Bar = 40 μ m.

54 pairs of marginal teeth. In 12 specimens of *Spiromoelleria quadrae*, there were 46 to 61 rows of teeth and marginal tooth counts of 56 to 78 pairs. For 13 specimens of *S. kachemakensis*, there were 37 to 64 rows of teeth and 43 to 73 pairs of marginal teeth.

Radulae of *Moelleria costulata* (Figure 2) and *Spiromoelleria quadrae* (Figure 3) are illustrated here. SEM illustrations of the radula of *S. kachemakensis* were not made, but the breadth of the rachidian tooth under the light microscope is comparable to that of *M. costulata* (Figure 2). The rachidian appears to be much less developed in *M. costulata* than in *S. quadrae*, but Hickman notes (personal communication) that failure of a shaft and cusp to develop fully is not unusual in many genera and may be characteristic of an entire species or sometimes only of some individuals. The morphology of the lateral and marginal teeth is similar in the two species. In both species, the first marginal is expanded at the base, representing a fusion of the first marginal with the lateromarginal plate. The particular form of the lateromarginal plate in these genera will be discussed in more detail elsewhere by Hickman.

Genus *Moelleria* Jeffreys, 1865

Moelleria JEFFREYS, 1865:292 [as *Mölleria*]. Type species by original designation: *Margarita costulata* Möller, 1842.

The generic and specific descriptions are combined under the species heading, as this genus is monotypic.

A monotypic genus is recognized on the basis of the unique shell sculpture—in which the axial ridges coalesce. Other trochaceans generally have collabral axial ribs, in which a complete rib is produced along the lip edge.

The original spelling *Mölleria* is correctly emended to *Moelleria*.

Moelleria costulata has a circumboreal distribution and

is well known, having been most recently discussed by FRETTER & GRAHAM (1977:93).

Moelleria costulata (Möller, 1842)

(Figures 2, 4)

Margarita costulata MÖLLER, 1842:81.

Adeorbis costulata: STIMPSON, 1851:32; GOULD, 1870:278, fig. 538.

Cyclostrema (*Margarita*) *costulata*: MÖRCH, 1857:10.

Mölleria costulata: JEFFREYS, 1865:291; DAUTZENBERG & FISCHER, 1912:261; THIELE, 1929:65; FRETTER & GRAHAM, 1977:93, figs. 71 (drawing of shell), 72 (SEM view of shell and protoconch).

Moelleria costulata: SARS, 1878:127, pl. 9, figs. 8a-c (shell), pl. III, figs. 5a-b (radula); BRÖGGER, 1901: pl. 12, figs. 4a-c.

Molleria costulata: MACGINITIE, 1959:1, pl. 3, figs. 2-5.

Moelleria costulata: ODHNER, 1912:19, pl. 5, figs. 43-47; ODHNER, 1915:152; THORSON, 1941:23; CLARKE, 1962: 13; MACPHERSON, 1971:29, pl. 2, fig. 5; ABBOTT, 1974: 61, fig. 501; WARÉN, 1980: pl. 11, fig. 1 (caption only); BAXTER, 1983:28.

Margarita minutissima MIGHELS, 1843:349, pl. 16, fig. 5; JOHNSON, 1949:227 (listed only); MACPHERSON, 1971: 29 (as probable synonym of *M. costulata*).

Margarites (*Margarites*) *minutissimus*: ABBOTT, 1974:37 (listed as valid species).

Description: Shell minute, turbate, deeply umbilicate; aperture and whorls circular; peritreme complete; suture deeply impressed. Whorls 3; sculpture of strong, flat-topped, slightly sigmoid axial ridges, some bifurcating below periphery; interspaces flat-bottomed, variable in width; spiral cords 0 to 9 (on Alaskan specimens), on base and umbilical wall only, variable in strength and spacing, forming nodes on crossing axial ribs. Surface dull, color uniformly brown, tan or gray. Operculum calcareous, exterior surface concave, with up to 6 evenly expanding



Explanation of Figures 4 to 6

Figure 4. *Moelleria costulata* (Möller, 1842). Three views of same specimen. LACM 73-23, 9 m off Hesketh Island, Kachemak Bay, Cook Inlet, Alaska. Height 2.04 mm, diameter 2.34 mm.

Figure 5. *Spiromoelleria quadrae* (Dall, 1897). Three views of same specimen. LACM 73-22, intertidal, Yukon Island, Ka-

chemak Bay, Cook Inlet, Alaska. Height 1.68 mm, diameter 2.46 mm.

Figure 6. *Spiromoelleria kachemakensis* spec. nov. Three views of holotype. LACM 1989, 9 m off Hesketh Island, Kachemak Bay, Cook Inlet, Alaska. Height 1.82 mm, diameter 2.24 mm.

volutions in multispiral pattern; interior surface flat, with same multispiral pattern.

Dimensions: Illustrated specimen (Figure 4): height 2.04 mm, diameter 2.34 mm. Shell height 87% of diameter.

Type material and type localities: *Moelleria costulata*, type not searched, type locality: Greenland (MÖLLER, 1842). *Margarita minutissima*, type not mentioned by JOHNSON (1949), presumably destroyed in the 1854 fire at Portland Society of Natural History; type locality: Casco Bay, Maine (MIGHELS, 1843).

Distribution: Circumboreal in the Arctic Ocean (MACGINITIE, 1959; MACPHERSON, 1971; ODHNER, 1912). Alaskan distribution from Attu, Aleutian Islands (LACM) (52°49'N, 172°10'E), to Turner Bay, Taku Inlet, southeastern Alaska (UAF) (58°19'N, 133°59'W). Atlantic distribution south to Maine, Greenland, Iceland, and Morocco (THORSON, 1941).

Habitat: On mud-gravel or mud-shell bottoms, 5 to 1943 m, occasionally common. Living specimens were reported off Point Barrow, Alaska, as deep as 200 m (MACGINITIE, 1959). THORSON (1941) reported a depth of 1943 m off

Morocco. There are, however, no records from such depths in Alaska. Living specimens of *Moelleria costulata* occurred with the type lot of *Spiromoelleria kachemakensis* in Kachemak Bay, Cook Inlet, Alaska.

Remarks: MACGINITIE (1959) detailed the extensive shell variation for this species occurring off Point Barrow, Alaska. Specimens from the Gulf of Alaska often lose the axial sculpture on the final whorl. The number of basal cords varies from 0 to 9.

ABBOTT (1974) listed *Margarites minutissima* Mighels as a good species. However, judging from the original illustration, it may clearly be assigned to the synonymy of *Moelleria costulata*, as suggested by MACPHERSON (1971).

Genus *Spiromoelleria* gen. nov.

Type species: *Moelleria quadrae* Dall, 1897. Alaska.

Description: Shell umbilicate; whorl circular in cross section; suture deeply impressed. Sculpture of regular spiral cords on entire body whorl and evenly rounded base; axial sculpture lacking. Calcareous operculum multispiral on both sides, not retractable deeper than aperture.

Spiromoelleria differs from *Moelleria* in lacking wavy axial sculpture. That there are two species is a strong point in support of the need for generic separation from *Moelleria*.

The two species of *Spiromoelleria* differ in shell proportions and in the strength of spiral sculpture. The distribution of this genus is limited to the northern Pacific.

Spiromoelleria quadrae (Dall, 1897)

(Figures 5, 7, 8)

"*Mölleria quadrae* Dall": NEWCOMB, 1896:19 [*nomen nudum*].

Moelleria quadrae DALL, 1897:15, pl. 1, figs. 14, 14a; WILLET, 1919:26; DALL, 1921:174; OLDROYD, 1924:170, pl. 44, figs. 7, 8.

Mölleria quadrae OLDROYD, 1927:171, pl. 91, figs. 11, 11a; KEEN, 1937:41; LAROCQUE, 1953:135.

Moelleria quadrae BURCH, 1946:26; EYERDAM, 1960:93; BERNARD, 1970:79; ABBOTT, 1974:61; GOLIKOV & GULBIN, 1978:183.

Moelleria (Spiromoelleria) quadrae: BAXTER, 1983:28.

Mölleria drusiana DALL, 1919:358; OLDROYD, 1927:172; KEEN, 1937:41; LAROCQUE, 1953:135.

Moelleria drusiana: DALL, 1921:174.

Moelleria drusiana: BURCH, 1946:26; EYERDAM, 1960:93; ABBOTT, 1974:61.

Description: Shell minute, depressed turbinata, broadly umbilicate; aperture and whorls circular, peritreme complete, suture deeply impressed, lip thin. Whorls 3.5; axial sculpture of weak, irregular growth increments only; spiral sculpture of variable number (49–77) of fine, narrow cords; spiral cords present throughout, from suture to umbilical walls, stronger on base, with wider interspaces on base. Color tan or whitish, rarely stained with rust. Oper-

culum calcareous, outer surface concave, with up to 6 evenly expanding volutions in multispiral pattern.

Dimensions: Illustrated specimen (Figure 5): height 1.68 mm, diameter 2.46 mm. Shell height 68% of diameter.

Distribution and habitat: North Pacific Ocean: Kuril Islands (GOLIKOV & GULBIN, 1978); Aleutian Islands (LACM: Attu, Amchitka); Kodiak Island (LACM); Kachemak Bay, Cook Inlet (RB, LACM); Prince William Sound (RB), Southeastern Alaska (WILLET, 1919); Cumsheewa Inlet, British Columbia (type locality). On undersides of rocks at low tide, on gravel or muddy, shell bottoms to 30 m. Common in intertidal zone in Kachemak Bay, Cook Inlet, Alaska; more frequent in the subtidal zone in southeastern Alaska. GOLIKOV & GULBIN (1978) reported it at 20 m, Simushir Island, Kuril Islands (approximately 47°N, 152°E).

Type material and type localities: *Moelleria quadrae*: USNM 107411, 18–27 m, Cumsheewa Inlet, Queen Charlotte Islands, British Columbia (approximately 53°N, 132°W); collected by C. F. Newcombe. *Moelleria drusiana*: USNM 31117, intertidal, Constantine Harbor, Amchitka Island, Aleutian Islands, Alaska; collected by W. H. Dall.

Remarks: Although DALL (1919) reported that *Moelleria drusiana* has the "surface smooth except for microscopic incremental lines," there are 42 fine spiral striae on the final whorl of the holotype. The holotype is clearly an immature specimen of *M. quadrae*, 1.1 mm in height and 1.5 mm in diameter.

Spiromoelleria kachemakensis

Baxter & McLean, spec. nov.

(Figures 1, 6, 9, 10)

Moelleria (Spiromoelleria) kachemakensis: BAXTER, 1983:28 [*nomen nudum*].

Description: Shell minute, turbinata, deeply umbilicate, aperture and whorls circular, peritreme complete, suture deeply impressed, lip thin. Whorls 3.4 to 3.7; axial sculpture of irregular growth increments only; spiral sculpture of 35–53 flat-topped cords on final whorl; spiral cords increasing in number by emergence between existing ribs; ribs faint near suture, strong and with narrow interspaces on upper surface of body whorl, with broader interspaces on lower surface. Color white to light tan, surface often stained rust to black. Operculum calcareous, multispiral, outer surface concave, with 6 evenly expanding volutions, not retracting within aperture.

Dimensions: Holotype: height 1.82 mm, diameter 2.24 mm; height 81% of diameter.

Type material: 12 live-collected specimens from the type locality, dredged by Baxter & McLean, 2 August 1973. Holotype LACM 1989; 5 paratypes LACM 1990, 2



Explanation of Figures 7 to 10

Figure 7. *Spiromoelleria quadrae* (Dall, 1897). Dorsal view, SEM. LACM 103331a, intertidal, Jakalof Bay, Kachemak Bay, Cook Inlet, Alaska. Height 1.48 mm, diameter 2.20 mm.

Figure 8. *Spiromoelleria quadrae* (Dall, 1897). Basal view, SEM. LACM 103331b, as same locality as Figure 7. Specimen subsequently lost.

Figure 9. *Spiromoelleria kachemakensis* spec. nov. Dorsal view, SEM. LACM 103332a, same locality as Figure 7. Height 1.80 mm, diameter 2.18 mm.

Figure 10. *Spiromoelleria kachemakensis* spec. nov. Basal view, SEM. LACM 103332b, same locality as Figure 7. Height 1.68 mm, diameter 2.06 mm.

paratypes CAS 029766, 2 paratypes USNM 804405, 2 paratypes NMC 86526, 1 paratype RB B461-12.

Type locality: 9 m on mud-shell bottom, off northwest side Hesketh Island, Kachemak Bay, Cook Inlet, Alaska (59°30'31"N, 151°30'01"W). The name of the species is based on the type locality.

Distribution: Kachemak Bay, Cook Inlet; along the Kenai Peninsula; Prince William Sound; east to Rush Bay, Glacier Bay, southeastern Alaska (58°28'N, 136°04'W) (UAF M2671, collected by George Mueller). Not collected at Kodiak Island or to the west. Living specimens have been collected by Baxter at or near the type locality and at Port Dick on the south side of the Kenai Peninsula (59°13'N, 151°03'W). Living on undersides of rocks at

low tide to 45 m on gravel or muddy, shell bottoms, particularly at the base of vertical drop-offs.

Remarks: *Spiromoelleria kachemakensis* has a higher spire (shell height 81% of diameter, compared to 68%), a narrower umbilicus, and more prominent spiral cords than *S. quadrae*. There are no intergrading specimens.

The small turbinid *Homalopoma lacunatum* (Carpenter, 1864), which occurs from Alaska to Washington, differs in having a larger, thicker shell, a less impressed suture and opercular volutions that are paucispiral.

We have no records of the three species occurring at the same station, as *Spiromoelleria quadrae* has been taken only intertidally and *Moelleria costulata* only subtidally in Kachemak Bay. However, *S. quadrae* and *S. kachemakensis* were collected together at low tide (near the type

locality of *S. kachemakensis*) at the west end of Yukon Island, Kachemak Bay (59°31.5'N, 151°29.5'W) by Baxter & McLean in August 1973. Living specimens of *M. costulata* were collected offshore with *S. kachemakensis* at the type locality.

MACNEIL *et al.* (1943) illustrated an eroded fossil specimen of *Spiromoelleria* from a raised terrace at Nome, Alaska, which they identified as "*Molleria* n. sp.?" Although its proportions are similar to those of *S. kachemakensis*, the specimen (USNM 499052) is much larger (dimensions: height 2.96 mm, diameter 3.40 mm) than known for *S. kachemakensis*. In size it is comparable to *Homalopoma lacunatum*, but it has the deeply impressed suture of the genus *Spiromoelleria*. We refrain from further treating this specimen in the absence of more and better preserved material.

ACKNOWLEDGMENTS

Collectors who have contributed to the distributional information recorded here include David Lindberg, George Mueller, Charles O'Claire, Paul Scott, and the late Robert Talmadge. We thank Joseph Rosewater (USNM) and Barry Roth (CAS) for access to collections. SEM photos of radulae were generously provided by Carole S. Hickman. Photographs of shells are the work of Bertram C. Draper. Paul Greenhall and Cynthia Gust (USNM) provided the SEM views of shells. We thank Eugene Coan and Carole Hickman for reading the manuscript and offering helpful suggestions.

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The Bernardinidae of the Eastern Pacific (Mollusca: Bivalvia)

by

EUGENE COAN

Research Associate, Department of Invertebrate Biology,
California Academy of Sciences, Golden Gate Park,
San Francisco, California 94118

Abstract. The Bernardinidae is a family of minute, shallow-water marine bivalves as yet known only from the eastern Pacific. They combine an internal ligament with three cardinal teeth in the left valve, two or three in the right, and at least one lateral tooth. The four known species brood their young. The family is here assigned to the Cyamiacea instead of where it has been placed in the Arctiacea.

In *Bernardina*, the anterior end is longer than the posterior; there is heavy concentric sculpture; and there is a large anterior lateral tooth, but no posterior lateral. *Bernardina bakeri* Dall, the type species, occurs from Pacific Grove, California, to Isla Natividad, Baja California Sur. *Bernardina margarita* (Carpenter) occurs from Isla Guadalupe, Baja California Norte, to Bahía Banderas, Jalisco, Mexico.

In *Halodakra*, the posterior end is longer than the anterior; the sculpture consists of fine concentric threads; and there is a posterior lateral tooth. *Halodakra*, s.s., lacks an anterior lateral tooth. *Halodakra* (*H.*) *subtrigona* (Carpenter), the type species, occurs from Tomales Bay, California, to Mancora, Peru. A new subgenus, *Stohleria*, is proposed for *H.* (*S.*) *salmonia* (Carpenter), which has an anterior lateral tooth. This species occurs from Brookings, Oregon, to Punta San Hipolito, Baja California Sur; *Crassatella marginata* Keep and *Psephidia brunnea* Dall are synonyms.

INTRODUCTION

I BECAME curious about the Bernardinidae when, during my review of the Crassatellinae of the eastern Pacific (COAN, 1984), I attempted to find a proper home for *Crassatella marginata* Keep, 1887. I concluded then and confirm now that it is a synonym of *Halodakra salmonia* (Carpenter, 1864). In arriving at this conclusion, however, I discovered that the two previously described species of *Halodakra* Olsson, 1961, are sympatric along much of the coast of southern California and Baja California Norte. Here I explain how they can be separated. I also provide characters differentiating the two species of *Bernardina* Dall, 1910. The distributions of all four species are documented, a neotype and four lectotypes are designated, and all four species are illustrated. The placement of the family within bivalves is also discussed.

CONVENTIONS AND ABBREVIATIONS

In the following treatment, each valid taxon is followed by a synonymy, information on type specimens and local-

ities, notes on distribution and habitat, and additional discussion.

The synonymies include all major accounts of the species, but generally not minor mentions in the literature. The entries are arranged in chronological order under each species-name, with changes in generic allocation from the previous entry, if any, and other notes provided in brackets after each entry.

The following are the abbreviations of institutions used in the text:

AHF—Allan Hancock Foundation, Los Angeles

BM(NH)—British Museum (Natural History), London

CASIZ—California Academy of Sciences, Department of Invertebrate Zoology, San Francisco

LACM—Los Angeles County Museum of Natural History

USNM—United States National Museum of Natural History Washington, D.C.

The thicknesses are of entire specimens with valves articulated unless stated otherwise. The proportions are based

on measurement of at least 10 specimens. A "pair" means the two valves of a single specimen.

Superfamily CYAMIACEA

Family BERNARDINIDAE Keen, 1963

Bernardinidae KEEN, 1963:91

The family Bernardinidae was proposed by KEEN (1963) for the eastern Pacific genera *Bernardina* and *Halodakra*. Later (KEEN, 1969:N650), she supplied a definition of the family.¹

The shells of species in this family are small to minute, attaining only about 4.5 mm in length. Sculpture consists of concentric threads or prominent concentric ribs. The hinge has an oblique resilium, well below the dorsal margin, in combination with two or three cardinal teeth in each valve and at least one lateral tooth. The pallial line is broad and entire. There is no evident lunule or escutcheon.

All four known species of the Bernardinidae occur in the eastern Pacific among rubble in rocky areas, from the intertidal area to subtidal depths; none has been recorded deeper than 60 m. All brood their young; I have observed broods in dried specimens of each of the four species.

This family has been placed in the Arcticea, members of which attain 50 to 100 mm in size, have an external ligament, and are not known to brood their young. I think a better placement would be in the Cyamiacea, which was most recently studied by PONDER (1971). Many members of this superfamily are small, have an internal ligament, and brood their young within their ctenidia. Among other known differences between these two superfamilies are the morphologies of the ctenidia. The Arcticea have plicate ctenidia with interlamellar septa (BOSS, 1982:1146); those of the Cyamiacea lack interlamellar septa and are not plicate (BOSS, 1982:1133).

Although most bernardinids are evidently not uncommon in shallow water, no preserved material is yet available for study. Observations on living or preserved specimens would considerably increase our knowledge about this family, including its taxonomic placement.

The two bernardinid genera are reminiscent of some species of the Veneridae in which the ligament may be somewhat sunken below the hinge margin and which brood their young. Frank BERNARD (1982:147) has recently proposed the genus *Nutricula* for one such venerid. Bernardinids can be distinguished from these small venerids by their lack of a pallial sinus, their proportionately less conspicuous beaks, and their internal ligament. *Bernardina* with its long anterior end is unlikely to be confused with other genera. *Halodakra* is most likely to be confused with

small specimens of the eastern Pacific venerid genera *Transennella*, *Nutricula*, *Pitar*, or *Psephidia*. In addition to the features given above, *Halodakra* has a posterior lateral tooth in its left valve and a slot for it in the right, features not present in these venerids.

The following is a key to the four species of the Bernardinidae:

- A. Anterior end longer than posterior; concentric sculpture of heavy ribs; posterior lateral tooth absent; 3 cardinals present in each valve *Bernardina*
 - (1) Prodissoconch set off by a prominent, raised ring; concentric ribs wide; proportionately higher ($l/h = 1.1$); attains 3 mm in length *B. bakeri*
 - (2) Prodissoconch set off by a low, raised ridge; concentric ribs narrow; lower ($l/h = 1.2$); minute, attains only 2.4 mm *B. margarita*
- B. Posterior end longer than anterior; concentric sculpture of fine threads; posterior lateral present; 3 cardinals in left valve, 2 in right *Halodakra*
 - (1) Left valve without an anterior lateral tooth; oval and elongate ($l/h = 1.3$); white, generally with a radial row of brown chevrons; attains 4.5 mm in length *H. (Halodakra) subtrigona*
 - (2) Left valve with an anterior lateral tooth, right valve with a slot for it; generally higher, trigonal ($l/h = 1.2$); entire shell white, salmon, or brown, without a radial row of brown chevrons; attains 4.3 mm in length *H. (Stohleria) salmonea*

Bernardina Dall, 1910

Bernardina DALL, 1910:171-172; type species (original designation): *B. bakeri* Dall, 1910.

Anterior end longer than posterior; sculpture of heavy concentric ribs; three cardinal teeth present in each valve; large anterior lateral present in left valve, well spaced from cardinals; no posterior lateral present.

Bernardina bakeri Dall, 1910

(Figures 1, 2)

Bernardina bakeri Dall, 1910

DALL, 1910:171-172

DALL, 1916a:24

DALL, 1921:30

OLDROYD, 1925:108-109; pl. 15, figs. 7, 8

EMERSON, in BURCH, 1944a:19; BURCH, 1944a:19

BURCH 1944b:7, 1 fig.; BURCH, 1945:11

BERNARD, 1983:49

Type material and locality

USNM 220099, **lectotype** (herein), a right valve; length, 2.5 mm; height, 2.2 mm; thickness, 0.7 mm (pair would have been 1.4 mm thick) (Figure 1). USNM 792413, **paralectotypes**, 7 pairs, 40 valves. The lectotype is the only specimen in the lot that comes close to the originally stated length of 2.8 mm.

¹ The family name is based on *Bernardina*, which DALL (1910) had dedicated to Felix Bernard, a pioneer worker on the development of the bivalve hinge.

Isla Coronado del Sur, Baja California Norte, Mexico (32°24'N, 117°15'W); 5.5 m; F. Baker.

Description

Small (to 3.0 mm in length; LACM 63-41, Middle Isla Coronado, Baja California Norte); triangular, length 1.1 times height; anterior end longer, rounded; posterior end slightly angled; inflated, thickness 0.5 times height. Surface with large, rounded concentric ribs that become broader ventrally; prodissococonch set off by a raised ring. Color white.

Right valve with a narrow anterior cardinal, a broad central cardinal, and a narrower posterior cardinal. Anterior end with a broad slot for lateral of left valve, distant from cardinals; both sides of slot swollen into teeth. Left valve with a narrow anterior cardinal, a broad central cardinal, and a very narrow posterior cardinal, the ligament just posterior to it. Anterior end with a large lateral, well spaced from cardinals (Figure 2).

Geographic distribution and habitat

Pacific Grove, Monterey Co., California (36°37'42"N, 121°54'48"W) (LACM 72-88), to Isla Natividad, Baja California Sur (27°52'N, 115°11'W) (LACM 72-116); intertidal area to 24 m, with a mean depth of 10 m; among rubble in rocky areas. Not uncommon; I have examined 47 lots. I have not located any specimens to confirm BURCH's (1944a:19) record from Bahía Magdalena, Baja California Sur, but the following species does occur there. Example of a lot with a brood: LACM 63-41.

This species has been reported from the Pleistocene of three of the Channel Islands of southern California: Anacapa (VALENTINE & LIPPS, 1963:1294, 1297) and San Nicolas (VEDDER & NORRIS, 1963:46-47, 50), both Ventura Co.; and Santa Barbara, Los Angeles Co. (LIPPS *et al.*, 1968:297, 299).

Bernardina margarita (Carpenter, 1857)

(Figures 3, 4)

Circe margarita Carpenter, 1857

CARPENTER, 1857a:247, 306 [*nomen nudum*]

CARPENTER, 1857b:81, 82

DALL, 1902b:408 [indeterminate juveniles]

KEEN, in BURCH, 1944b:17 [juvenile venerids]

HAAS, 1945:4-5 [indeterminate juveniles]

PALMER, 1951:20 [*Circe*]

KEEN, 1958:140 [juveniles, possibly venerids]; 622

[*Lasaea*]

BRANN, 1966:34, pl. 9, fig. 114 [*Circe*]

KEEN, 1968:394, 395, fig. 4 [*Bernardina*]

KEEN, 1971:118, 117, fig. 264

BERNARD, 1983:49

Type material and locality

BM(NH) 1857.6.4.412, lectotype (KEEN, 1968), pair; length, 1.15 mm; height, 0.95 mm; thickness, 0.8 mm

(Figure 3). Other specimens now in lot, paralectotypes, one minute pair, 1 left valve. USNM 715784, paralectotypes, 3 valves.

Mazatlán, Sinaloa, Mexico (23°12'N, 106°25'W); F. Reigen, 1848-1850.

Description

Minute, smaller than *Bernardina bakeri* (to 2.4 mm in length; LACM 72-121, Isla Guadalupe, Baja California Norte); trigonal, but slightly more elongate than *B. bakeri*, length 1.2 times height; anterior end longer, sharply rounded; posterior end quadrate; inflated, thickness 0.5 times height. Surface with conspicuous concentric ribs, finer than those in *B. bakeri*; prodissococonch set off by a ridge less prominent than that in *B. bakeri*. Color white, tan, pink, or brown, sometimes with lighter blotches; more colorful than *B. bakeri*.

Hinge very similar to that of *B. bakeri*² (Figure 4).

Distribution and habitat

Northwest side of Isla Guadalupe, Baja California Norte (29°11'18"N, 118°15'12"W) (LACM 72-121), in the Gulf of California as far north as Guaymas, Sonora (27°58'N, 111°11'W) (LACM 68-13), and southward to Bahía Banderas, Jalisco (20°32'N, 105°19'W) (LACM 69-18 & 71-83), all in Mexico; intertidal area to 21 m, with a mean depth of 16 m; in rubble in rocky areas. Not common; I have examined only 21 lots. Example of a lot with a brood: LACM 72-121.

Discussion

This species was proposed in the genus *Circe* SCHUMACHER, 1817 (pp. 50, 152), which is now placed in the Veneridae. However, CARPENTER (1857b) realized that his new species had an internal ligament, and he placed *Circe* in the Astartidae.

Halodakra Olsson, 1961

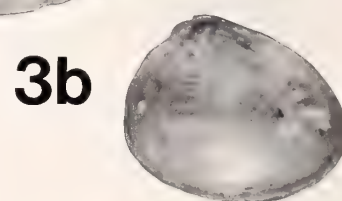
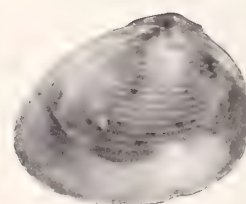
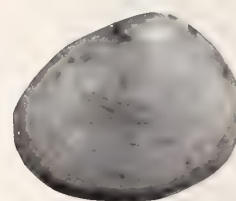
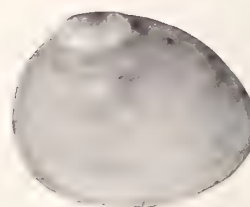
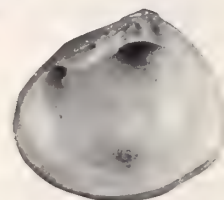
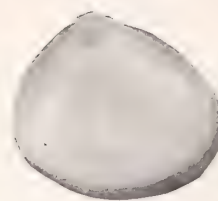
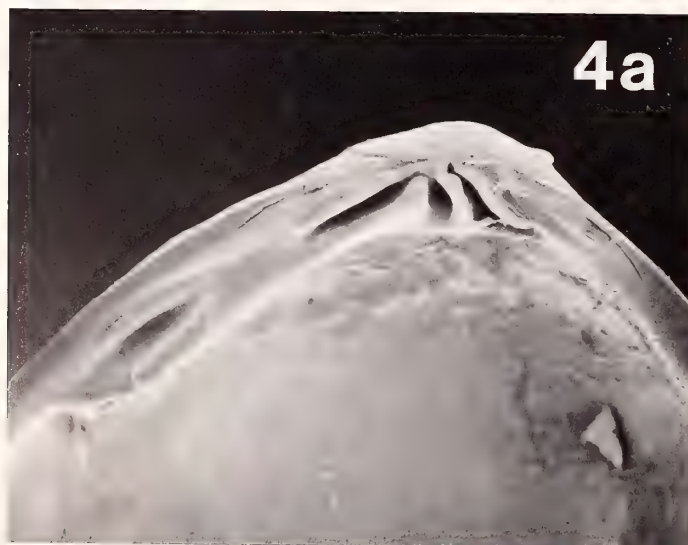
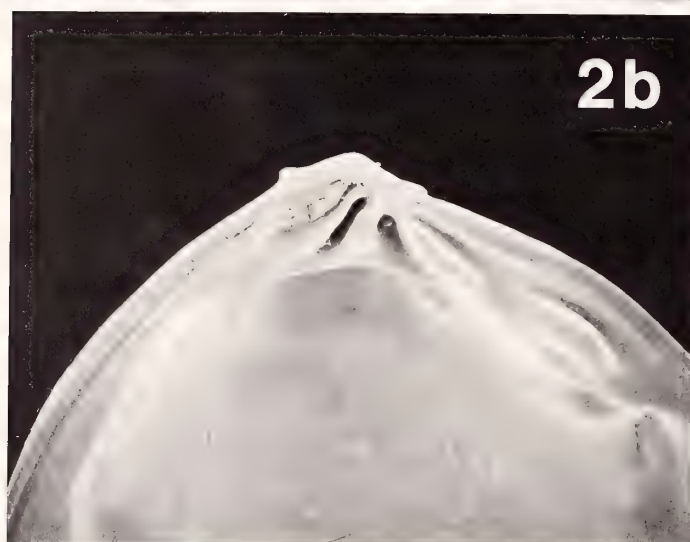
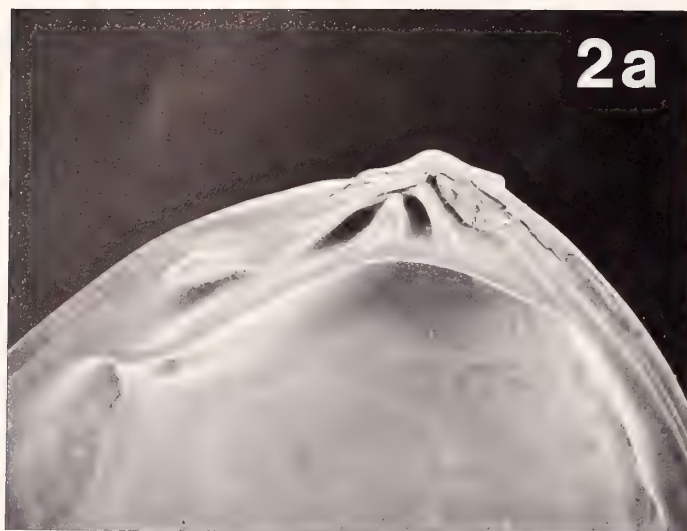
Halodakra OLSSON, 1961:319, 472; type species (original designation): ?*Circe subtrigona* Carpenter, 1857.

Posterior end longer than anterior; sculpture of fine concentric threads; three cardinal teeth present in the left valve, two in the right; posterior lateral present in the left valve, a socket for it in the right. The name means "sea tear."

(*Halodakra*)

Without an anterior lateral tooth.

² KEEN (1971:118) described this species as having two cardinal teeth in the right valve, but like *B. bakeri*, it has three cardinal teeth in each valve.



Halodakra (Halodakra) subtrigona (Carpenter, 1857)

(Figures 5-7)

Circe subtrigona Carpenter, 1857CARPENTER, 1857a:247, 306 [*nomen nudum*]

CARPENTER, 1857b:82 [“?Circe”]

DALL, 1902b:408 [indeterminate juveniles]

KEEN, in BURCH, 1944b:18 [possibly juvenile *Petricola*]HAAS, 1945:4-5 [*Semele*]

PALMER, 1951:20 [“?Circe”]

KEEN, 1958:140 [*Circe*, but indeterminate juveniles], 622 [*Psephidia*]OLSSON, 1961:319, 500 (pl. expl.), pl. 27, figs. 1-1c [*Halodakra*]

BRANN, 1966:34, pl. 9, fig. 115 [“?Circe”]

KEEN, 1968:394, 396 [*Halodakra*]

KEEN, 1971:118, 117, fig. 265

BERNARD, 1983:49

Type material and locality

BM(NH) 1857.6.4.413, **lectotype** (herein), pair; length, 2.4 mm; height, 1.9 mm; thickness, 1.4 mm (Figure 5). Other specimens in this lot, **paralectotypes**, 2 pairs, one right valve. Field Museum of Natural History, Chicago, 6698, **paralectotype**, right valve (HAAS, 1945: 5). USNM 715785, **paralectotypes**, 1 pair, 10 valves. Mazatlán, Sinaloa, Mexico (23°12'N, 106°25'W); F. Reigen, 1848-1850.

Description

Small (to 4.5 mm in length; LACM 71-83, Los Arcos, Bahía Banderas, Jalisco, Mexico); ovate, length 1.3 times height; anterior end sharply rounded; posterior end longer, broadly rounded; anterior end more expanded dorsally than that in *Halodakra salmonea*; inflated, thickness 0.7 times height. Surface with fine concentric striae. White to light brown, with dark brown flecks or chevrons in a radial row from beaks toward ventral margin posterior to midline, often interspersed with white material; light brown zig-zag lines also present on external surface in many specimens. Dark brown color present on hinge anterior and posterior to umbones.

Right valve with a broad, elongate anterior cardinal and a thin posterior cardinal, the resilifer posterior to it; elongate slot present for anterior cardinal of left valve; slot for posterior lateral of left valve still more elongate, its ventral edge swollen to form a tooth. Left valve with an elongate anterior cardinal, a short central cardinal, and a

very thin posterior cardinal; ligament just posterior to the latter; posterior end with a lateral tooth³ (Figure 7).

Geographic distribution and habitat

Tomales Bay, Marin Co. (38°15'N, 123°W) (AHF 1628-48), and Southeast Farallon Id., San Francisco Co. (37°41'N, 123°W) (LACM 62-9), California, to and throughout the Gulf of California, to El Rubio and Punta Mero, Tumbes Prov., Peru (3°54'S, 80°53'W) (LACM 72-85); Mancora, Tumbes Prov., Peru (4°6'S, 81°4'W) (OLSSON, 1961); intertidal area to 24 m, with a mean depth of 9 m; among rubble in rocky areas. Not uncommon; I have examined 102 lots. Example of a lot with a brood: LACM 63-11.

Discussion

This species has not previously been reported from California, specimens having been confused with *H. salmonea*.

Specimens from central California are elongate and oval. They lack the characteristic radial row of dark brown flecks, but similar specimens occur in southern California and northern Baja California Norte along with more typical specimens. Material from central California is rare in museums (only three lots), with no material in collections from between Carmel and Corona del Mar. It is possible that when more material is available for study, two taxa of *Halodakra*, *s.s.*, will come into focus. I have illustrated here (Figure 6) an elongate, oval specimen from central California.

***Stohleria* Coan, subgen. nov.**

Type species: *Psephis salmonea* Carpenter, 1864.

Differing from *Halodakra*, *s.s.*, in the presence of an anterior lateral tooth in the left valve and a slot for it in the right valve.

The name of this subgenus honors Dr. Rudolf Stohler, the founding editor of the journal *The Veliger*.

³ OLSSON (1961) terms the broad anterior cardinal of the right bivalve as “bifid.” His figure of the left valve seems to show a cardinal tooth posterior to the ligament, but I see none there in the material I have examined. He judges the combination of what I consider the central and the posterior cardinals of the left valve to be a single, bifid tooth.

Explanation of Figures 1 to 4

Figures 1 and 2. *Bernardina bakeri* Dall.

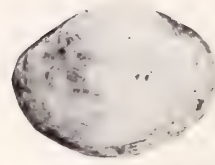
Figure 1. **Lectotype** (herein). USNM 220099, length, 2.5 mm, outside and inside views.

Figure 2. LACM 67-1, Puerto Santo Tomás, Baja California Norte, 3-8 m, length, 2.8 mm. 2a, right valve. 2b, left valve.

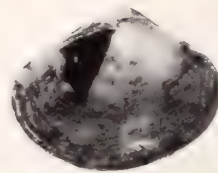
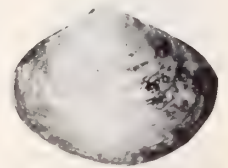
Figures 3 and 4. *Bernardina margarita* (Carpenter).

Figure 3. **Lectotype** of *Circe margarita* Carpenter, BM(NH) 1857.6.4.412, length, 1.15 mm. 3a, outside views. 3b, inside views.

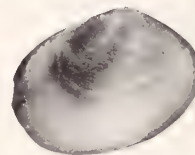
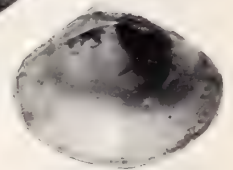
Figure 4. LACM 71-14, Punta Entrada, Bahía Magdalena, Baja California Sur, 3-15 m, length, 2.0 mm. 4a, right valve. 4b, left valve.



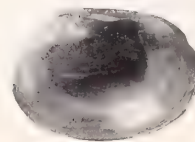
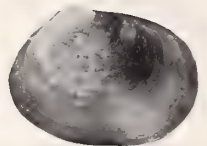
5a



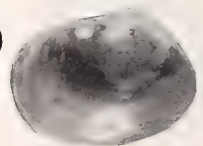
5b



6a



6b



Halodakra (Stohleria) salmonea (Carpenter, 1864)

(Figures 8–10)

Psephis salmonea Carpenter, 1864

- CARPENTER, 1864:539, 611, 641 [1872:25, 97, 127]
 CARPENTER, 1866:209
 ARNOLD, 1903:18, 21, 37, 52, 75, 152
 DALL, 1902b:408 [juvenile *Tivela*]
 DALL, 1916a:34 [“*Psephidia*”]
 DALL, 1921:44 [“*Psephidia*”]
 OLDROYD, 1925:162 [*Psephidia*; incorrectly cites a figure of *Tellina salmonea*]
 GRANT & GALE, 1931:338 [*Psephidia*]
 BURCH, 1944c:16; BURCH, 1945:16
 PALMER, 1958:16, 20, 22, 37, 99, 336 (pl. expl.), pl. 11, figs. 6–12 [*Psephidia*]
 BERNARD, 1983:49 [*Halodakra*]
Crassatella marginata Keep, 1887
 KEEP, 1887:179 [AS “CARPENTER”] [KEEP, 1888, 1892, 1893:179]
 PAETEL, 1890:139
 KEEP, 1904:50, 281
 KELSEY, 1907:38 [*Crassatella*]
 KEEP, 1911:61–62
 ORCUTT, 1915:13 (1st sect.), 60 (2nd sect.)
 LAMY, 1917:204
 KEEP & BAILEY, 1935:73 [*Crassatellites*]
 BURCH, 1944b:9 [*Crassatellites*]; SMITH, in BURCH, 1944b:9 [unidentifiable]; KEEN, in BURCH, 1944b:17 [*Crassatella*; probably synonym of *Psephidia brunnea*]
 PALMER, 1958:81
 BERNARD, 1983:36 [synonym of *Eucrassatella fluctuata* (Carpenter, 1864)]
 COAN, 1984:164 [*Halodakra*; possibly synonym of *H. salmonea*]
 “*Crassatellites margarita* Carpenter,” auctt., non *Circe margarita* Carpenter, 1857b
 JORDAN, 1924:153
 ?“*Tivela marginata* Carpenter,” auctt.
 DALL, 1902b:386
 BERRY, 1907:20
 LAMY, 1917:204
 PALMER, 1958:96
Psephidia brunnea Dall, 1916
 DALL, 1916a:34 [nomen nudum]
 DALL, 1916b:413
 DALL, 1921:44
 OLDROYD, 1925:162
 KEEN, in BURCH, 1944b:17
 BURCH, 1944c:16; BURCH, 1945:16
 KEEN, 1971:118 [*Halodakra*]
 BERNARD, 1983:49 [synonym of *Halodakra salmonea*]

Type material and localities

Psephis salmonea—USNM 15578, **lectotype** (herein), pair; length, 3.0 mm; height, 2.7 mm; thickness, 2.0 mm (Figure 8). From Calif. State Geol. Surv. Coll. no. 1068. San Diego, San Diego Co., California (about 32°33'N, 117°14'W; J. G. Cooper, probably Nov. or Dec. 1861. **Paralectotypes**: Redpath Museum, McGill University 115, 5 specimens; Santa Catalina Id., Los Angeles Co., California (about 33°26'N, 118°29'W); 55 m; J. G. Cooper, June 20–26, 1863.

Crassatella marginata—The original type material has not been located in the parts of the Keep collection now housed at the University of California at Berkeley (D. Lindberg, verbal communication, Jan. 1983), the California Academy of Sciences (B. Roth, verbal communication, Jan. 1983), or the Institute of Geology & Paleontology of Tohoku Univ. in Sendai, Japan (Ogasawara, *in litt.*, 5 Sept. 1983). **Neotype**: USNM 15578, the lectotype of *Psephis salmonea*, which gives it the same type locality.

Psephidia brunnea—USNM 109469, **lectotype** (herein), pair; length, 3.3 mm; height, 2.8 mm; thickness, 2.0 mm (Figure 9). **Paralectotypes**, USNM 792512, 1 broken and 4 entire pairs. Santa Catalina Island, Los Angeles Co., California (about 33°26'N, 118°29'W); 29 m.

Description

Small (to 4.3 mm; LACM 67-61; Isla San Jeronimo, Baja California Norte); ovate to almost triangular, length 1.2 times height; posterior end longer; anterior and posterior ends rounded to sharply rounded; inflated, thickness 0.7 times height; beaks produced, more so than in *Halodakra (H.) subtrigona*. Shell surface with fine concentric striae. Color white, salmon, to brown, with darker brown dorsally on either side of beaks, often with light brown patches or wavy lines, which may also be visible on internal surface.

Right valve with a broad anterior cardinal and a narrower posterior cardinal, the ligament well posterior to it. Anterior end with an elongate slot for anterior cardinal and anterior lateral of left valve, with distinct pits for each of these teeth; ventral edge of this slot swollen to form a lateral tooth; posterior end with an elongate slot for posterior lateral of left valve, its ventral margin swollen into

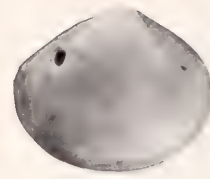
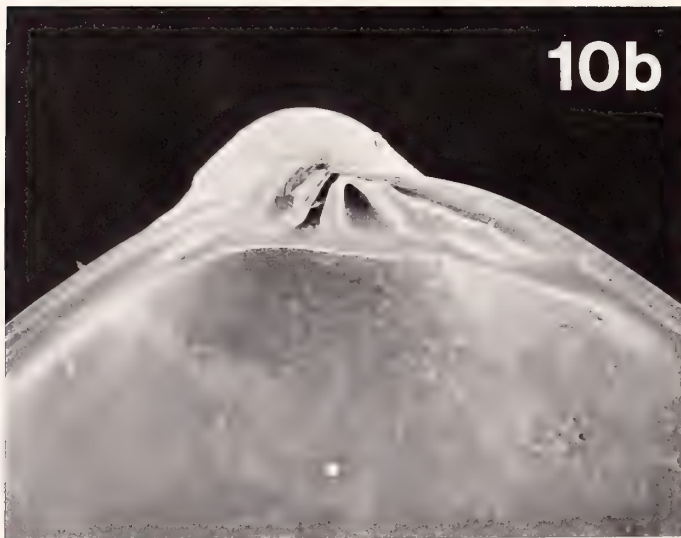
Explanation of Figures 5 to 7

Figures 5 to 7. *Halodakra (Halodakra) subtrigona* (Carpenter).

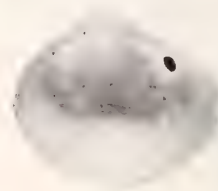
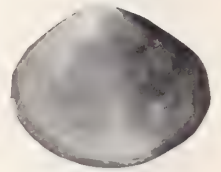
Figure 5. **Lectotype** (herein) of *Circe subtrigona* Carpenter, BM(NH) 1857.6.4.413, length 2.4 mm. 5a, outside views 5b, inside views.

Figure 6. LACM 66-57, Carmel, California, intertidal area, length, 2.5 mm. 6a, outside views. 6b, inside views.

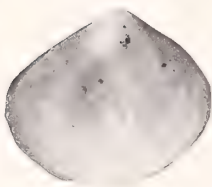
Figure 7. LACM 71-151, northeastern end of Isla Cedros, Baja California Norte, 6–12 m, length, 2.2 mm. 7a, right valve. 7b, left valve.



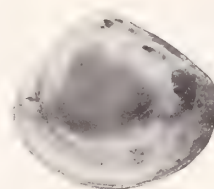
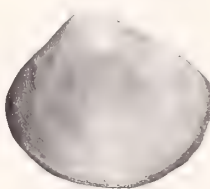
9a



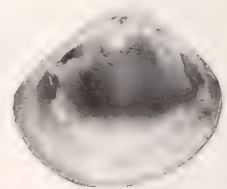
9b



8a



8b



a lateral tooth. Left valve with a medium-sized anterior cardinal, a medium-sized central cardinal, and a very thin posterior cardinal bordering resilium. Anterior end with a conspicuous lateral tooth, generally in line with anterior cardinal. Posterior end with an elongate lateral (Figure 10).

Geographic distribution and habitat

Brookings, Curry Co., Oregon (42°2'42"N, 124°17'12"W) (LACM 63-35), to Punta San Hipolito, Baja California Sur (26°58'N, 114°W) (USNM 127538; CASIZ 039005); intertidal area to 60 m, with a mean depth of 16 m; in gravel and rubble in rocky areas. Not uncommon; I have studied 74 lots. Example of a lot with a brood: LACM 63-50.

YOCUM & EDGE (1929:50) reported "*Psephidia brunnea* Dall" from Coos Bay, Oregon, farther north than Brookings. However, it is more likely that they had either *Nutricula tantilla* (Gould, 1853) or *Psephidia lordi* (Baird, 1863), small venerids that occur there but are not present on their faunal list. Their specimens have not been located at the University of Oregon (P. Frank, *in litt.*, 5 Jan. 1984).

VEDDER (1960:326) reported "*Psephidia* cf. *P. salmonea*" from a Pliocene sandstone in Orange Co., California. ARNOLD (1903: see synonymy) reported this species from what is now regarded as the Lower Pleistocene of Santa Barbara and of San Pedro, California. DELONG (1941: facing p. 244) also recorded it from the latter.

Discussion

This species was first proposed in the venerid genus *Psephis* Carpenter, 1864, which proved to be a homonym (*non Psephis* GUÉNÉE, 1854:257) and was renamed *Psephidia* by DALL (1902a:243). It is unclear why Dall failed to compare his new species, *Psephidia brunnea*, to *P. salmonea*, having placed them side by side in the same genus.

As discussed elsewhere (COAN, 1984), *Crassatella marginata* Keep, 1887, was most probably based on specimens of *Halodakra* from southern California.⁴ Keep credited this species to Carpenter, but Carpenter never proposed it. The name probably originated from the miscopying of a label by Carpenter with some southern Californian specimens of *Halodakra salmonea* that had been misidentified

by him as "*Crassatella margarita* (Carpenter, 1857)" (CASIZ 036681). The latter species is a Panamic *Bernardina* discussed herein.

BERNARD (1983:36) recently associated Keep's taxon with the rare, deep water Californian *Eucrassatella fluctuata* (Carpenter, 1864). This is unlikely because Keep had several specimens, and the *Eucrassatella* is still known from only a few specimens, none resembling the "pin-head"-sized material that Keep said he had. Moreover, Keep's description demonstrates that he had good, probably live-collected material showing a color pattern.

I now recognize two species of *Halodakra* in southern California, and it is difficult to be certain which of the two Keep had. However, it is probable that he had *H. salmonea*, the more common of the two forms there. The neotype designation herein therefore serves to eliminate future doubt and speculation.

It is uncertain what GARDNER (1917:113, pl. 4, fig. 12) reported and illustrated from Laguna Beach, California, as "*Crassatella marginata*." It could have been either species of *Halodakra*, and efforts to trace the specimens have been unsuccessful (Oglesby, *in litt.*, 25 Jan. 1984).

ACKNOWLEDGMENTS

I thank the personnel of the following institutions who made material available for study: James H. McLean and Gale Sphon of the Los Angeles County Museum of Natural History, Solene Morris of the British Museum (Natural History), Joseph Rosewater of the United States National Museum of Natural History, Barry Roth and Robert Van Syoc of the California Academy of Sciences, Paul Scott of the Santa Barbara Museum of Natural History, Anthony D'Attilio of the San Diego Natural History Museum, David Lindberg of the University of California at Berkeley, and Mary Garback of the Academy of Natural Sciences of Philadelphia.

I thank Bertram C. Draper for the photographs of type specimens and Mary Ann Tenorio for the SEM photographs of the hinges. Robin Senour mounted the plates.

I appreciated comments on my manuscript by Barry Roth, James McLean, Myra Keen, and Paul Scott, and advice on aspects of this project by Peter Frank, Carole M. Hertz, Kanshiro Ogasawara, and Larry C. Oglesby.

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All works cited in the text, including sources of taxonomic units are listed. Volume, bulletin, monograph, memoir, and professional paper numbers are in bold face; series

Explanation of Figures 8 to 10

Figures 8 to 10. *Halodakra* (*Stohleria*) *salmonea* (Carpenter).

Figure 8. **Lectotype** (herein) of *Psephis salmonea* Carpenter, and **neotype** (herein) of *Crassatella marginata* Keep, USNM 15578, length, 3.0 mm. 8a, outside views. 8b, inside views.

Figure 9. **Lectotype** (herein) of *Psephidia brunnea* Dall, USNM 109469, length 3.3 mm. 9a, outside views. 9b, inside views.

Figure 10. LACM 71-151, northeastern end of Isla Cedros, Baja California Norte, 6-12 m, length, 2.8 mm. 10a, right valve. 10b, left valve.

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A Technique for Determining Apparent Selective Filtration in the Fresh-water Bivalve *Elliptio complanata* (Lightfoot)

by

COLIN G. PATERSON

Department of Biology, Mount Allison University,
Sackville, New Brunswick, Canada E0A 3C0

Abstract. *Elliptio complanata* (Lightfoot) filtering natural lake water shows a marked selectivity for smaller particles. Selection is for particle size rather than type as similar results were obtained when the bivalves were held in suspensions of animal charcoal. Filtration rate varies with particle abundance with the highest rates occurring at intermediate particle densities.

INTRODUCTION

AN EXTENSIVE literature exists on the filtration rates of marine bivalves as modified by a variety of extrinsic factors. Many of these studies have determined filtration rate from the rate of disappearance from the medium of organic and/or inorganic particles of a limited size range and of fixed abundance. Such determined values have only restricted applicability unless it is assumed that particle size and abundance do not modify apparent filtration rate. In contrast, numbers of authors have shown that measured filtration rate varies with particle size (VAHL, 1973; BAYNE *et al.*, 1977), abundance (RICE & SMITH, 1958; ALI, 1970; TENORE & DUNSTAN, 1973; FOSTER-SMITH, 1975; WIDDOWS *et al.*, 1979), and type (size?)(RICE & SMITH, 1958).

Studies on fresh-water unionid bivalves are sparse in comparison with those on marine species. ALLEN (1914), using *Lampsilis luteolus*, and DE BRUIN & DAVIDS (1970), using *Anodonta cygnea*, measured pumping rate by a direct method. SALANKI & LUKACSOVICS (1967) determined the rate of uptake of neutral red stain in *Anodonta cygnea*. Neither of these techniques is suitable for determining the effect of particle size, abundance, or type on filtration rate. LEWANDOWSKI & STANCZYKOWSKA (1975) used an indirect method to obtain limited results on filtration rates of *Anodonta piscinalis* and *Unio tumidus*.

The present study was undertaken to determine whether a species of fresh-water unionid bivalve, *Elliptio complanata* (Lightfoot), would show responses to variations in particle size, abundance, and type, as has been found in many marine species.

MATERIALS AND METHODS

During the summer months, specimens of *Elliptio complanata* were collected by dragging in Morice Lake, a relatively old (ca. 1765) polymictic, mesotrophic reservoir located approximately 3 km north of Sackville, New Brunswick, Canada. The collecting site is described in more detail by SEPHTON *et al.* (1980). At a shore laboratory, specimens were placed in a 55 × 115 cm polyethylene tank with an outlet drain located 30 cm above the bottom. Natural lake water was continuously pumped from an inlet located 20 cm above the lake bottom 15 m from the shore and supplied to the holding tank at a rate of 75 L/h. Aeration was continuous. Experiments were conducted in six plastic containers measuring 27.5 × 23.5 cm and having a depth of 14 cm. Containers were equipped with outlet valves 8.5 cm from the container bottom through which water samples were obtained. Six liters of freshly pumped lake water were added to each container. Five specimens of *E. complanata* with a maximum length of 6–7 cm were gently scrubbed and placed into each of four containers. The remaining containers served as controls.

At the initiation of the experiment, 50 mL water samples were removed through the outlet of each container and diluted 1:1 with an electrolyte solution; then, 2 mL samples were passed through a 200 μ m aperture of a model TAI Coulter Counter equipped with a Population Mode. In all cases, triplicate particle counts were taken and averaged. This procedure was then repeated after 2 h. When a particle passes through the aperture it is counted as well as being assigned to one of 14 channels (channel

Table 1

Particle size distribution as monitored by the Coulter Counter using a 200 μm aperture.

Channel	Mean geometric volume (μm^3)	Minimum volume (μm^3)	Minimum diameter (μm)
3	47.39	33.51	4.00
4	94.78	67.02	5.04
5	189.6	134.0	6.35
6	379.1	268.1	8.00
7	758.3	536.2	10.08
8	1516	1072	12.70
9	3033	2145	16.00
10	6066	4289	20.20
11	12.13×10^3	8579	25.40
12	24.27×10^3	17.16×10^3	32.00
13	48.54×10^3	34.31×10^3	40.30
14	97.18×10^3	68.63×10^3	50.80
15	194.4×10^3	137.3×10^3	64.00
16	388.7×10^3	274.5×10^3	80.60

3 through channel 16) based on particle size. The mean geometric volume, minimum volume, and minimum diameter of the particles measured by each channel when a 200 μm aperture is used are given in Table 1. Because particle counts in channels 7 to 16 were too low to accurately determine filtration rate these particle counts were pooled. Background count due to the electrolyte solution was determined and suitable corrections made. Details on the application of the Coulter Counter to research of this nature may be found in SHELDON & PARSONS (1977), MAYZAUD & POULET (1978), POULET (1978), and HARBISON & McALISTER (1979).

At the end of an experiment, the length (L) of each bivalve in a container was determined to the nearest 0.5 mm using calipers, and the individual dry tissue weight (W) was determined from the regression equation:

$$\log_{10} W \text{ (g)} = -2.403 + 2.770 \log_{10} L \text{ (cm)}$$

(CAMERON & *et al.*, 1979). Individual weights in each container were averaged and filtration rate determined as mL/g/h for this average weight using the formula:

FR (mL/g/h)

$$= \frac{\log_e P_0 - \log_e (P_t^T + (P_0^c - P_t^c)) \times V \text{ (mL)}}{2 \times 5 \times \bar{W} \text{ (g)}}$$

where P = particles/mL, 0 = time 0, t = time 2 h, c = control, T = test, V = volume (mL), \bar{W} = average dry tissue weight (g), and FR = filtration rate (mL/g/h).

Temperature was monitored in all experiments and ranged from a low of 19.0°C to a high of 22.7°C. No corrections have been attempted for these minor fluctuations. The containers were not aerated during the experiments as this would re-suspend pseudofaeces. This pro-

duces a possible error due to natural particle settling which is corrected for by determining the decline in the number of particles in each channel in the control containers.

This experimental approach was repeated on 18 occasions during the summer, and some variability in absolute filtration rates was observed which could have been a product of either fluctuations in particle abundance or in the nature of the particles. During August when the lake water remained at a relatively constant temperature of about 20°C, natural lake water was filtered through 3.0- μm Millipore filters and the filtrate used to make four dilutions of lake water. Two experiments were conducted each day. Each experiment consisted of two replicates of each of two of the particle densities and an appropriate control for each density. A total of eight replicates were determined for natural lake water and for each of the four dilutions. The sequence of replicates was staggered over the 10 days of the experiment in order to compensate for minor changes in particle concentration of the lake water during this period of time.

In an attempt to determine whether the apparent higher filtration rates observed for smaller particles was a product of reduced particle size or a result of the nature of the particles, further experiments were conducted in which technical animal charcoal was used to make a dense suspension in 3.0 μm filtered lake water. Amounts of suspension were added to containers of 6 L of 3.0 μm filtered lake water to produce a total particle count approximating 13,000 particles/mL. Five bivalves between 6 and 7 cm in length were added to each of four containers while the other two remained as controls. This experiment was replicated five times.

RESULTS

During the summer, filtration rate as determined from total particle counts or counts from specific channels showed little variation on any one day and often remained relatively constant over several days of stable weather. However, over the course of the summer, fluctuation in filtration rate did occur which might relate to seasonal or storm-induced changes in abundance and/or nature of the particles. When all data are pooled and the filtration rate in each channel changed to a percentage of the filtration rate calculated from channel 3 (Figure 1), a significant linear decline in relative filtration rate is found which can be adequately described by the equation: $\text{RFR} = 176.8 - 23.95N$ ($n = 67$, $r = 0.89$, $P < 0.001$) where RFR is the relative filtration rate expressed as a percentage of that determined for channel 3 and N is the channel number. For the pooled 7–16 channels, channel 7 was used. The fitted line passes through the mean value for all channels except 3. That some curvilinearity exists between channels 3 and 4 is apparent from the intercept at channel 3, where the calculated RFR is 104.95%, although all observed filtration rates for this channel were set at 100%. As shown in Table 1, the mean geometric volume doubles

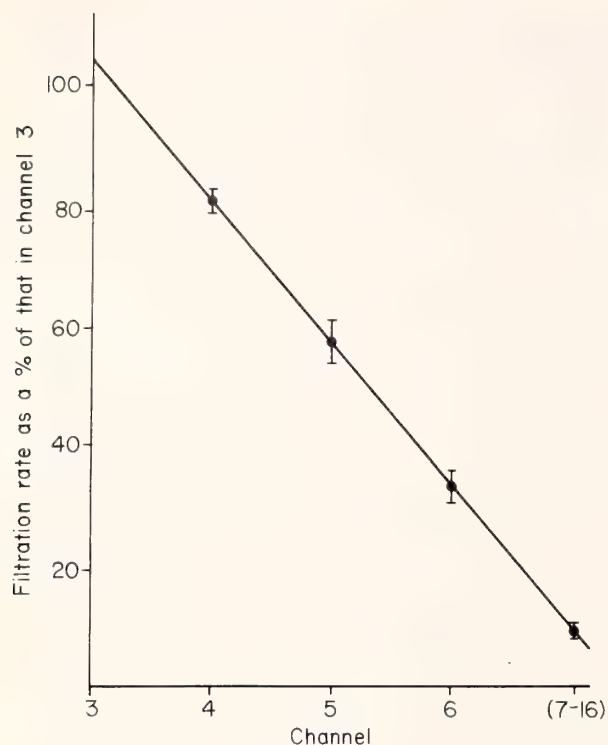


Figure 1

Elliptio complanata. Apparent filtration rate for each channel number expressed as a percentage of that determined for channel 3. Vertical bars represent one standard error about the mean.

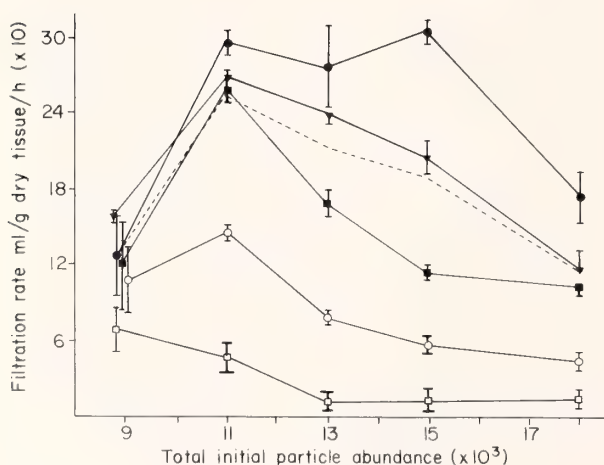


Figure 2

Elliptio complanata. Apparent filtration rates for total particle counts (dashed line), channel 3 (●), channel 4 (▼), channel 5 (■), channel 6 (○) and pooled results from channels 7 through 16 (□).

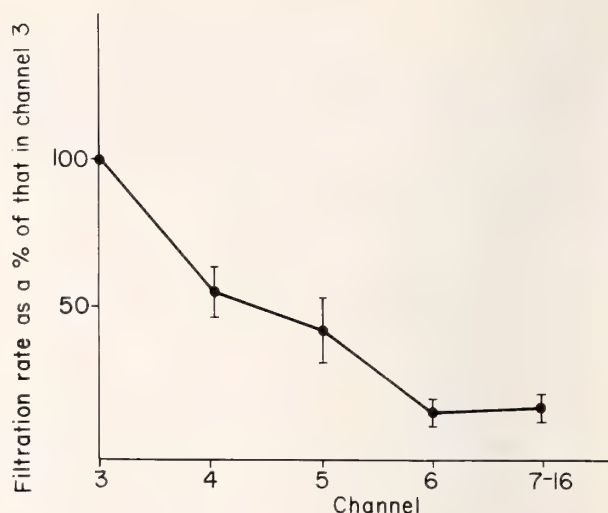


Figure 3

Elliptio complanata. Apparent filtration rates of technical animal charcoal expressed as a percentage of that determined for channel 3. Vertical bars represent one standard error about the mean.

from one channel to the next. Thus, a negative exponential decline in relative filtration rate occurs which is well described by the equation: $RFR = 230 - 76.3 \log_{10} V$, where V is the mean geometric volume for the channel. The number of particles in channel 7 is always substantially higher than in 8 through 16 so a mean geometric volume of $758.3 \mu m^3$ was used for this channel group.

To test the possible effect of particle abundance on the variation observed over the summer, lake water collected over a limited time period was used to determine filtration rate in the unmodified water and in four dilutions (Figure 2). At the lowest seston concentration, all channels produced relatively similar filtration rate values. This might be brought about by a reduced pumping rate, which allows more time for successful filtration of the larger particles. An increase in average initial particle abundance to 11,000/mL caused a maximum filtration for most channels. Further increases in particle abundance resulted in a decline in the apparent filtration rate as calculated from particle uptake in all channels with the exception of channel 3. Filtration calculated for counts in this channel remained relatively constant over the particle range of 11,000–15,000/mL and then declined. The decreasing filtration rate with increasing channel number and, thus, particle size (Figures 1, 2) could result either from some active or passive "selection" operating on particle size as such or from selection on the nature of the particles. Figure 3 shows the results obtained when apparent filtration rate was determined using animal charcoal. A significant decline in apparent filtration rate occurs as the particle size increases from channel 3 through channel 6 and then remains constant.

DISCUSSION

The filtration activities of *Elliptio complanata*, at least as measured under summer conditions, show many patterns that are similar to those of marine filter-feeding bivalves. As found for marine forms by RICE & SMITH (1958), TENORE & DUNSTAN (1973), FOSTER-SMITH (1975), and WIDDOWS *et al.* (1979), filtration rate is lower at low particle concentrations and then increases to a peak value. After this peak is reached, there is then a decline as particles increase in abundance.

Like many marine bivalves (VAHL, 1973; BAYNE *et al.*, 1977), *Elliptio complanata* also appears to show pronounced selectivity. One obvious difference is that in the marine species selectivity appears to be for particles with equivalent spherical diameters between about 6 and 10 μm . In *Elliptio complanata* the selection is most definitely for the smaller particle sizes with the highest filtration rates normally being found for channel 3, which measures particles with diameters between 4.00 and 5.05 μm . The results of the studies using animal charcoal suggest that the selection is a passive one based on particle size and not particle nature. If selection is passive for a particular particle size, then it is interesting to interpret further the results found in this and other studies where filtration rate initially increases as particle abundance increases and then decreases. Results such as those presented in Figure 2 could be explained on the basis of either changes in the efficiency of particle retention or changes in actual pumping rate. Although both mechanisms may well be operational, it would appear that changes in pumping rate can at least partially explain the results. As shown in Figure 2, the apparent filtration rates at the lowest particle density were very similar for channels 3, 4, 5, and 6. At the highest particle densities, the filtration rates, as measured from these channel counts, began to approach some degree of similarity. It might well be that, at low particle density, water is pumped at a lower rate which allows more time for actual filtration and, consequently, particles of all sizes are retained efficiently. With an increase in particle abundance, pumping rate increases. At this increased rate, smaller particles are retained more effectively than larger particles. JORGENSEN (1983) has argued that, in marine filter feeders, an increase in the velocity of water passing over the gill mechanisms, which would result from an increased pumping rate, increases the efficiency of retention of smaller particles relative to larger ones. Perhaps when the particle density becomes great enough, there is no advantage in using energy to maintain an elevated pumping rate, as a much reduced pumping rate will still produce adequate food supplies.

It is apparent from the results of this study that the determination of an accurate measure of filtration rate is extremely difficult. To determine filtration activities of a species such as *Elliptio complanata*, it would be necessary to measure filtration in the natural seston suspensions of the habitat. The apparent filtration rate would have to be determined for essentially all particle sizes that the bivalve

can effectively remove from the water. This would then allow determination of the total amount of material removed from the water in a given period of time. This study also would have to be expanded to cover the seasonal changes in the abundance and size distribution of the lake seston.

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NOTES, INFORMATION & NEWS

California Malacozoological Society, Inc., is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed January 6, 1964 in the office of the Secretary of State). The Society publishes a scientific quarterly, *The Veliger*. Donations to the Society are used to pay a part of the production costs and thus to keep the subscription rate at a minimum. Donors may designate the Fund to which their contribution is to be credited: Operating Fund (available for current production); Savings Fund (available only for specified purposes, such as publication of especially long and significant papers); Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

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Another Generous Donation by the San Diego Shell Club

Our faithful friends in the San Diego Shell Club have made another sizable gift to *The Veliger* Endowment Fund. Since the income from this fund is intended for the purpose of keeping our publication and membership costs as low as possible, this generous donation is all the more gratefully received. We are pleased to thank the San Diego Shell Club once again for its considerate contribution toward our continuing activities.

Reprints, Page Charges, and Donations

While it was hoped at the "birth" of *The Veliger* that a modest number of reprints could be supplied to authors free of charge, this has not yet become possible. Reprints are supplied to authors at cost, and requests for reprints should be addressed directly to the authors concerned. The Society does not maintain stocks of reprints and also cannot undertake to forward requests for reprints to the author(s) concerned.

Although many scientific journals assess page charges, the Executive Board of our Society, for the time being at least, wishes to avoid this possible financial handicap to the younger contributors. However, because of the high

cost of halftone plates, a suitable contribution to reimburse the Society must be sought. Similarly, contributions will be sought from authors (or preferably their institutions) to help defray costs of line drawings and tables in excess of four simple ones. We emphasize, however, that requests for donations are totally unrelated to acceptance or rejection of manuscripts for *The Veliger*. Acceptance is entirely on the basis of merit of the manuscript. Donations are to be made after publication, if at all, and are strictly on a voluntary basis.

Nevertheless, donations by authors and readers are necessary for the continued good health of our Society, the stated aim of which is to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible. Authors and readers are reminded that contributions to the C.M.S., Inc. are deductible by donors as provided in section 170 of the Internal Revenue Code (for Federal income tax purposes).

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If your address is changed it will be important to notify us of the new address at least six weeks before the effective date and not less than *six weeks* before our regular mailing dates. Send notification to C.M.S., Inc., P.O. Box 9977, Berkeley, CA 94079.

Because of a number of drastic changes in the regulations affecting second class mailing, there is now a sizable charge to us on the returned copies as well as for our remailing to the new address. We are forced to ask our members and subscribers for reimbursement of these charges; further, because of increased costs in connection with the new mailing plate, we also must ask for reimbursement of that expense. The following charges must be made:

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Supplements available from C.M.S.

Supplement to Volume 3:

[Part 1: Opisthobranch Mollusks of California by Prof. Ernst Marcus;

Part 2: The Anaspidea of California by Prof. R. Beeman, and the Thecosomata and Gymnosomata of the California Current by Prof. John A. McGowan]

Supplement to Volume 11:

[The Biology of Acmaea by Prof. D. P. Abbott *et al.*, ed.]

Supplement to Volume 14:

[The Northwest American Tellinidae by Dr. E. V. Coan]

Supplement to Volume 16:

[The Panamic-Galapagan Epitoniidae by Mrs. Helen DuShane]

Supplement to Volume 17:

[Growth Rates, Depth Preference and Ecological Succession of Some Sessile Marine Invertebrates in Monterey Harbor by Dr. E. C. Haderlie]

Our stock of this supplement is exhausted. Copies may be obtained by applying to Dr. E. C. Haderlie, U.S. Naval Post-Graduate School, Monterey, CA 93940.

Supplements not available from C.M.S.

Supplements to Volume 7 (Glossary) and 15 (Ovulidae) are sold by 'The Shell Cabinet,' P.O. Box 29, Falls Church, VA 22046; supplement to Volume 18 (Chitons) is available from 'The Secretary,' Hopkins Marine Station, Pacific Grove, CA 93950.

WE ARE PLEASED to announce that an agreement has been entered into by the California Malacozoological Society, Inc. with Mr. Steven J. Long for the production and sale of microfiche reproductions of all out-of-print editions of the publications of the Society. The microfiches are available as negative films (printed matter appearing white on black background), 105 mm × 148 mm and can be supplied immediately. The following is a list of items now ready:

Volume 1 through Volume 6: \$9.00 each.

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California residents please add the appropriate amount for sales tax to the prices indicated.

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Volumes and Supplements not listed as available in microfiche form are still available in original edition from C.M.S. Orders should be sent directly there.

Single Copies of THE VELIGER

We have on hand some individual copies of earlier issues of our journal and are preparing a list of the various issues available with the prices. Some issues are present in only one or two copies, while others may be present in 10 or more copies. As we are anxious to make room, we will offer these numbers at an exceptionally low price. This list may be obtained by sending a self-addressed, stamped envelope to C.M.S., Inc., Post Office Box 9977, Berkeley, CA 94709. Foreign correspondents should enclose one international postal reply coupon.

Second International Cephalopod Symposium

The Second International Cephalopod Symposium will be held in Tübingen, Federal Republic of Germany from 16-23 July 1985. It is intended to bring together zoologists and paleontologists working on cephalopods, and the following themes have been proposed: major evolutionary strategies, strategies in early development, migration and global distribution, dietary habits and locomotion, post-

mortem processes, and buoyancy, vertical migration and tiering in the water column. Several field trips are scheduled to occur before and after the sessions.

For further details, write to Prof. Jürgen Kullmann, Geol.-Paläont. Institut, Sigwartstr. 10, D-7400 Tübingen, Federal Republic of Germany.

BOOKS, PERIODICALS & PAMPHLETS

Illustration of the Types Named by S. Stillman Berry in his "Leaflets in Malacology"

by CAROLE M. HERTZ. 10 January 1984. The Festivus, volume 15, supplement. 42 pp., 92 figs. \$5.00 plus \$0.88 postage and California sales tax where applicable. (copies available from the San Diego Shell Club, Inc., % 3883 Mt. Blackburn Ave., San Diego, California 92111).

How often, since Dr. Stillman Berry began his series of "Leaflets," have collectors and other students of west American malacology complained because there were no figures of the newly-described shells. At long last that lack is remedied in a thoroughgoing way. Publication of the figures simply had to wait until there came on the scene the right combination of talents: photographers like Leroy Poorman with the skill and the patience to search out and make color slides of the holotypes, David Mulliner, who could turn these into creditable black-and-white prints, and an author, Carole Hertz, with the willingness not only to get the illustrations together but also to compile, with the complete list of species, the supplementary data that are important to the systematist—(1) where are these specimens now; (2) what synonyms have been suggested; and (3) what are the titles among the "Leaflets" that carry descriptions by Stillman Berry of new species. Carole Hertz is highly to be commended for having carried through this project in so efficient a way. She has provided also an alphabetical index to the species names, a list of the new genera described by S. S. Berry in the "Leaflets," a three-page bibliography, and a tabular summary of the eight species of *Octopus* that were not practicable to be illustrated here.

This paper should win a niche for itself as one of the significant modern contributions to west coast malacology.

Myra Keen

Distribution of Shallow-water Marine Mollusca, Yucatan Peninsula, Mexico

by HAROLD E. VOKES & EMILY H. VOKES. 1983. Middle American Research Inst., Tulane Univ., New Orleans, Louisiana. Mesoamerican Ecol. Inst., Monogr. 1:viii + 183 pp., 50 pls. \$21.50.

This is an illustrated checklist based on collections by the late archaeologist E. Wyllys Andrews, IV, to whom

the work is dedicated, and by the Vokes themselves. Some 769 intertidal and shallow-water species are reported from the seven regions the authors identify on the peninsula. Special lists highlight the taxa most characteristic of the entire peninsula and of the north and west coasts, which are on the Gulf of Mexico, and the east coast, which is on the Caribbean.

Each species is well illustrated, mostly by photographs, though not necessarily of specimens from Yucatan. In the systematic list, the original reference and combination are given, as well as a second reference, generally to Abbott's *American Seashells* (1974). Very few taxonomic and nomenclatural remarks are in this list. A second table gives the occurrence of the species in the seven regions, with an indication of their relative abundance in the collections. No habitat information is presented.

This checklist should prove useful both to visitors to this area as well as to specialists wanting some information about this previously poorly studied peninsula.

E. V. Coan

Proceedings of the Second Franco-British Symposium on Molluscs

ALAN BEBBINGTON (editor). Proceedings of the Second Franco-British Symposium on Molluscs. *Journal of Molluscan Studies*, Supplement 12A:227 pp. Priced at 30 pounds (20 pounds to members of the Malacological Society of London). Copies may be purchased from The Editor, *Journal of Molluscan Studies*, Dept. of Zoology, Univ. of Reading, Whiteknights Park, Reading, Berkshire, U.K.

The majority of papers delivered at the Second Franco-British Symposium on Molluscs, held in London from 6 to 9 September 1982, are presented in this special supplement to the *Journal of Molluscan Studies*. The volume contains 36 papers (29 in English, 7 in French) and 12 posters (10 in English, 2 in French). Mollusks from many parts of the world are represented, including a few from the eastern Pacific, and the papers cover a wide range of topics, including evolution, biogeography, ecology, behavior, physiology, and anatomy. In short, something is here for everyone interested in mollusks.

D. W. Phillips

Manuscripts

Manuscripts must be typed on white paper, 8½" by 11", and double-spaced throughout (including references, figure legends, footnotes, and tables). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (SMITH, 1951), for two authors (SMITH & JONES, 1952), and for more than two (SMITH *et al.*, 1953).

The "literature cited" section must include all (but not additional) references quoted in the text. References should be listed in alphabetical order and typed on sheets separate from the text. Each citation must be complete and in the following form:

a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra*. *Veliger* 4:132–134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. *Living marine molluscs*. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135. *In*: R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal invertebrates of California*. Stanford Univ. Press: Stanford, Calif.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend.

Figures and plates

Figures must be carefully prepared and should be submitted ready for publication. Each should have a short legend, listed on a sheet following the tables.

Text figures should be in black ink and completely lettered. Keep in mind page format and column size when designing figures.

Photographs for half-tone plates must be of good quality. They should be trimmed off squarely, arranged into plates, and mounted on suitable drawing board. Where necessary, a scale should be put on the actual figure. Preferably, photographs should be in the desired final size.

It is the author's responsibility that lettering is legible after final reduction (if any) and that lettering size is appropriate to the figure. Charges will be made for necessary alterations.

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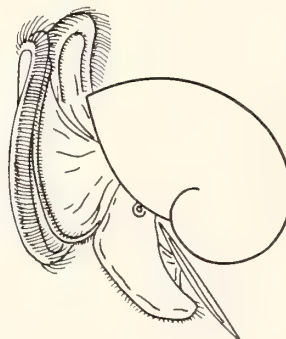
Receipt of a submitted manuscript, except in the case of foreign authors, is not acknowledged unless a stamped, self-addressed envelope is enclosed. Upon receipt each manuscript is critically evaluated by at least two referees. Based on these evaluations the editor decides on acceptance or rejection. Acceptable manuscripts are returned to the author for consideration of comments and criticisms, and a finalized manuscript is sent to press. The author will receive from the printer two sets of proofs, which should be corrected carefully for printing errors. At this stage, stylistic changes are no longer appropriate, and changes other than the correction of printing errors will be charged to the author at cost. One set of corrected proofs should be returned to the editor.

An order form for the purchase of reprints will accompany proofs. If reprints are desired, they are to be ordered directly from the printer.

Send manuscripts, proofs, and correspondence regarding editorial matters to: Dr. David W. Phillips, Editor, 2410 Oakenshield Road, Davis, CA 95616 USA.

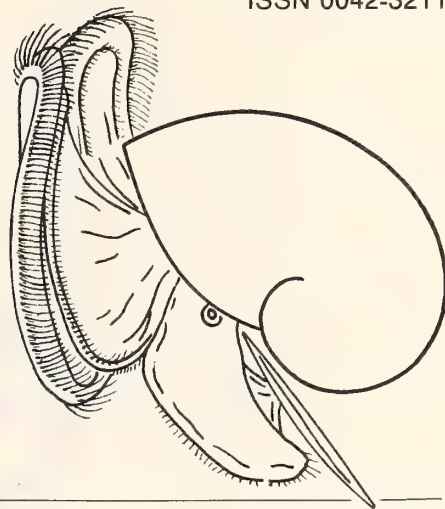
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Form, Function, and Origin of Temporary Dwarf Males in *Pseudopythina rugifera* (Carpenter, 1864) (Bivalvia: Galeommatacea)

by

DIARMAID Ó FOIGHIL

Department of Biology, University of Victoria, Victoria, British Columbia V8W 2Y2, Canada

Abstract. Female *Pseudopythina rugifera* (Carpenter, 1864) typically house a dwarf male within their mantle cavity. Dwarf males show considerable morphological differences from females. The dwarf male shell (<1.25 mm in length) is poorly developed, and a thin extension of the mid-mantle fold, bearing sensory papillae, covers the valves. The foot has a sucker-like ventral surface, is hypertrophied, and dorsoventrally compressed. Only one demibranch is present in the gills, and the visceral mass contains a fully functional digestive system, as well as a relatively large testis. Larger male individuals (2-5 mm in length) do not demonstrate sexual dimorphism and occur external to females. Some individuals are hermaphroditic and all specimens >6 mm in length are female. Available data suggest that *P. rugifera* is a protandrous hermaphrodite, with the dwarf male stage located inside the female mantle cavity; further development, incorporating morphological changes and eventual sex reversal, occurs external to the female host. Dwarf males may provide an efficient method of sperm transfer where space restrictions in habitats normally prevent the co-occurrence of equal-sized adult conspecifics of an outcrossing species. In the Galeommatacea, species with protandrous consecutive hermaphrodites or with complemental males may be the immediate evolutionary precursors of the dwarf male condition.

INTRODUCTION

THE TERM "dwarf male" describes cases where miniature males occur in or on a female (TURNER & YAKOVLEV, 1983). With the exception of the terebratulid *Zachsisia zenkewitschi* Bulatoff & Rjabtschikoff, 1933, dwarf males in the Bivalvia are restricted to a few galeommatacean species (TURNER & YAKOVLEV, 1983). JENNER & MCCRARY (1968) briefly describe the dwarf males of three species: *Montacuta percompressa* Dall, 1899, *Orobitella floridana* (Dall, 1899), and an undescribed species of *Entovalva*. *Pseudopythina subsinuata* (Lischke, 1871) is a protandrous hermaphrodite, the male stage being closely associated with females and, when very small, males are occasionally found within the mantle cavity of females (MORTON, 1972). Adult female *Ephippodonta* (*Ephippodontina*) *oedipus* Morton, 1976, typically possess two dwarf males in a pair of pallial pouches (MORTON, 1976). *Chlamydoconcha orcutti* Dall, 1884, and *Montacuta* (*Tellimya*) *phascolionis* Dautzenberg

& Fischer, 1925, have also been reported to have dwarf males (MORTON, 1981; DEROUX, 1960); however, because they occur in association with hermaphrodites rather than females, they may be more accurately classified as complemental males (see Discussion).

Pseudopythina rugifera, also placed in the genus *Neaeromya* (ABBOTT, 1974), is a relatively rare bivalve found in the northeastern Pacific from Alaska to Lower California (ABBOTT, 1974). ROSEWATER (1984) should be consulted for the most recent evaluation of the *Pseudopythina*-*Neaeromya*-*Orobitella* species complex. Typically, *P. rugifera* occurs as an ectocommensal, attached by byssus to one of three host species, the mudshrimp *Upogebia pugettensis* (Dana, 1852) or to two polychaete species, *Aphrodita japonica* Marenzeller, 1879 and *Aphrodita negligens* Moore, 1905 (PETTIBONE, 1953; MACGINITIE & MACGINITIE, 1968). The female morphology has been described in detail by NARCHI (1969), who found no males.

The morphology of dwarf male *Pseudopythina rugifera*

is described here, and the possible factors leading to the development of dwarf males in the Galeommatacea are discussed.

MATERIALS AND METHODS

A total of 24 specimens of *Pseudopythina rugifera* (not including dwarf males) was obtained between October 1983 and June 1984. All but one individual were attached to specimens of *Aphrodita japonica* or *A. negligens*, which were dredged off San Juan Island, Washington State, U.S.A. The polychaete hosts were then kept in an aquarium at the Friday Harbor Laboratories for up to six months (R. Strathmann, personal communication). One specimen of *P. rugifera* was retrieved attached to the mudshrimp *Upogebia pugettensis* in Bamfield Inlet, on the west coast of Vancouver Island, B.C., Canada, in April 1984 (D. Denning, personal communication). The specimens of *P. rugifera* were examined using a dissecting microscope and sexed by way of gonad squashes. Dwarf males present were removed from the female hosts and measured with an ocular micrometer. For optical histology, specimens were relaxed in 6.7% $MgCl_2$, fixed in 5% glutaraldehyde (biological grade), dehydrated in an ethanol series, embedded in JB4 resin, sectioned at 2 μm , and stained in Gill's haematoxylin and eosin. For scanning electron microscopy, specimens were fixed in a 3:1 mixture of 4% glutaraldehyde and 1% osmium tetroxide in 3% NaCl (SMITH, 1983), dehydrated in acetone, critical point dried, gold coated, and viewed with a JEOL JSM-35 scanning electron microscope. To investigate sperm ultrastructure, specimens were fixed in 5% glutaraldehyde in 0.1 M cacodylate buffer with 0.25 M sucrose, post-fixed with osmium tetroxide in the same buffer, dehydrated in ethanol, embedded in epon, and sectioned on a Reichert ultramicrotome. Silver-gray sections were stained with uranyl acetate and lead citrate and viewed with a Phillips EM 300 transmission electron microscope.

RESULTS

Sixteen of the 24 individuals obtained were female, 4 were male, 3 were hermaphroditic and one specimen did not exhibit any gonad development. When dissected, 11 of the 16 females (including the specimen retrieved from *Upogebia pugettensis*) contained one, and one female contained two, dwarf males within their mantle cavity. Data on the size frequency and sex of the specimens are presented in Figure 1. All individuals <1.25 mm in valve length were dwarf males occurring within the mantle cavity of female hosts. All individuals >6 mm in length were females, and specimens intermediate in size were male, hermaphroditic, or displayed no gonadal development.

Dwarf Male Morphology

The valves are poorly developed and gape widely; the valve margins make contact only at the hinge line (Figure

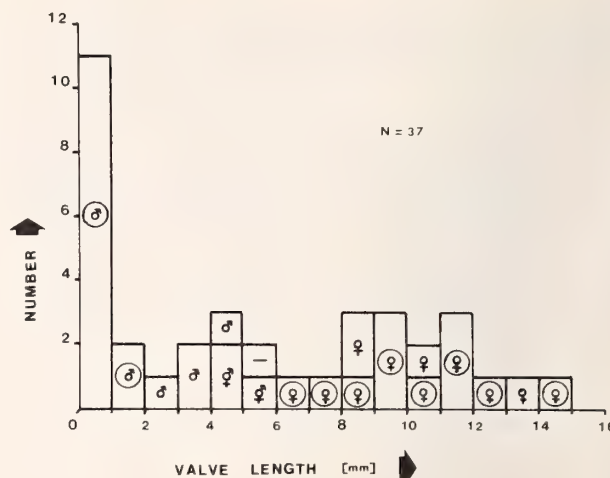


Figure 1

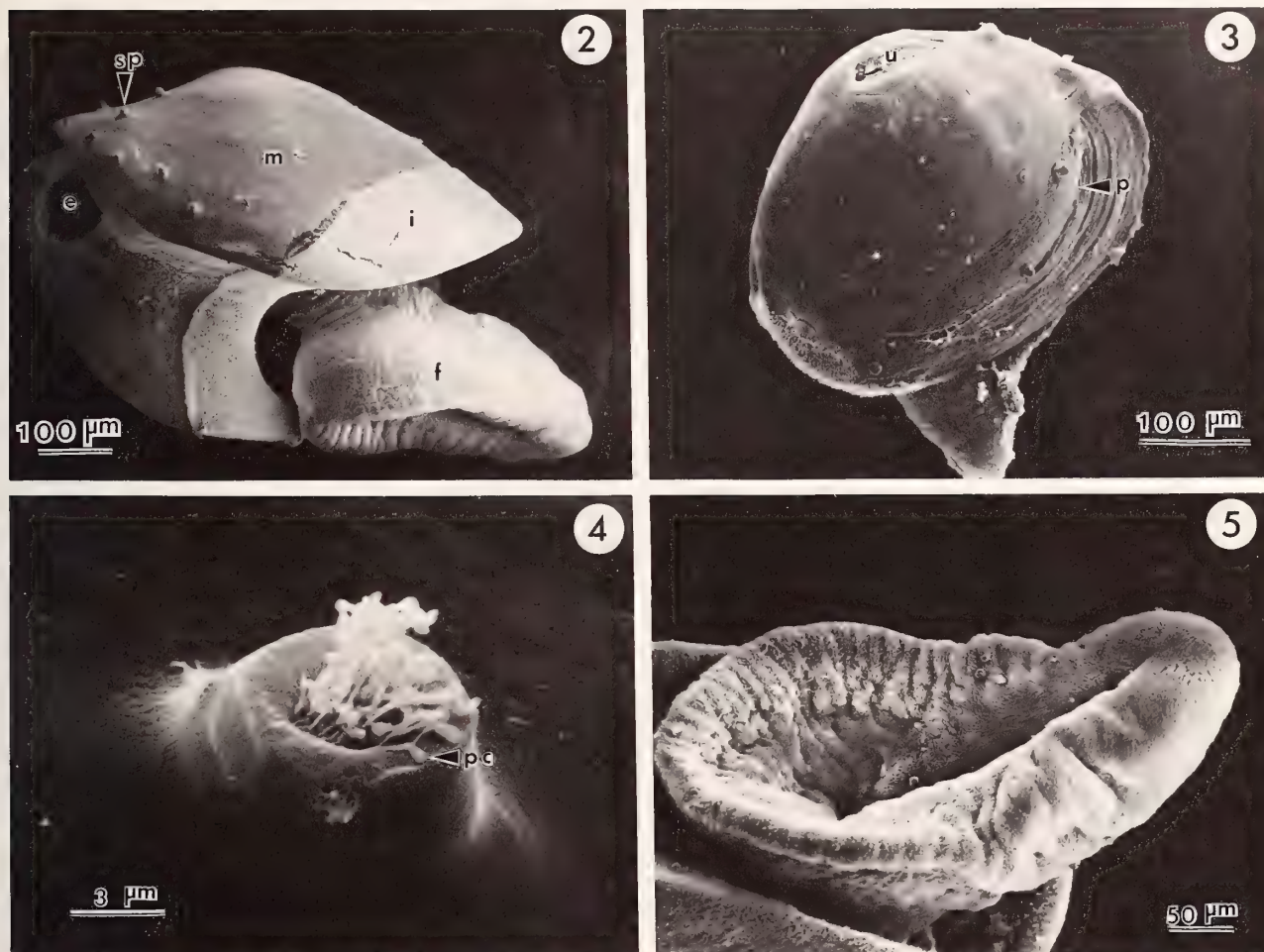
Length frequency and sex of *Pseudopythina rugifera* sampled. ♂, dwarf males; ♂, males external to females; ♀, hermaphrodites; ♀, females containing dwarf males; ♀, females not containing dwarf males; —, no gonad development.

2). The shell is whitish in color and semi-transparent. A prominent prodissococonch was present in all specimens (Figure 3) and ranged in length from 280 to 350 μm . The dissoconch bears concentric rings and faint radial lines.

An anterior pedal (inhalant) opening is separated from a slitlike posterior exhalant opening by the extensive fusion of the inner mantle fold (Figure 2). A shorter tract of fusion occurs dorsally, anterior to the hinge. The mid-mantle fold extends as a thin flap (1 or 2 cells thick) to cover the external surface of the shell (Figures 2, 3, 6). Papillae bearing apical tufts of cilia are present in this extension (Figure 2). These cilia exhibit bulbous tips when viewed by scanning electron microscope (Figure 4) and resemble paddle cilia (TAMARIN *et al.*, 1974), which have been recorded from a wide variety of taxa and are thought to have a sensory function (MATERA & DAVIS, 1982). In the smaller specimens, the mid-mantle fold does not fully cover the shell (Figure 3).

One of the most striking aspects of the dwarf male morphology is the foot. It is hypertrophied, dorsoventrally compressed, and cannot be withdrawn inside the shell. A pleated posterior heel region is distinct from the non-pleated anterior of the foot, and the ventral surface contains a prominent ventral groove (Figure 5). The animals are mobile; however, some individuals were attached by byssus to the mantle of the female. The other dwarf males were moving around the mantle cavity of their female hosts.

The gills contain one demibranch, each composed of a descending lamella only. No food groove is present, and the lamellae fuse together medially behind the foot (Fig-



Explanation of Figures 2 to 5

Figure 2. Scanning electron micrograph of *Pseudopythina rugifera* relaxed in 6.7% MgCl_2 . e, exhalant siphon; f, foot; i, inner mantle fold; m, mid-mantle fold; sp, sensory papillae.

Figure 3. Scanning electron micrograph of unrelaxed *Pseudopythina rugifera* dwarf male. p, prodissoconch-dissoconch interface; u, umbone.

Figure 4. Scanning electron micrograph of *Pseudopythina rugifera* dwarf male sensory papilla. pc, paddle cilia.

Figure 5. Scanning electron micrograph of *Pseudopythina rugifera* dwarf male foot.

ure 6). The lamellae also fuse for much of their length with the mantle.

A fully functional alimentary canal, containing esophagus, stomach, style sac, digestive gland, and intestine is present.

Each of the dwarf males examined possessed a testis, although it differed in the degree of development. The smallest individual (325 μm in length) contained two small, dorsal follicles with early gametogenic stages (spermatogonia and spermatocytes). In larger animals the entire posterior region of the visceral mass was composed of a bilobed testis, consisting predominantly of mature sperm

(Figure 6). This suggests that spermatogenesis is initiated at an early stage, and that it is a continuous process. Two dwarf males occurring inside newly spawned females appeared spawned-out, with the testis containing some residual sperm.

Pseudopythina rugifera sperm consist of a conical head 5.3 μm in length and a flagellum (Figure 7). The acrosome is apical, does not have an axial rod, and contains a U-shaped, membrane-bound vesicle surrounding a lumen of flocculent material (Figure 8). Four mitochondria in the middle piece surround a pair of centrioles. Sperm morphology in this species is typical of the primitive level of

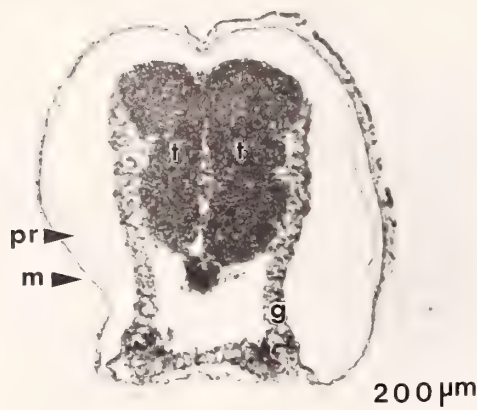


Figure 6

Light micrograph of a cross section through a dwarf male *Pseudopythina rugifera*. g, gills; m, mid-mantle fold; pr, periostracum; t, testis.

organization generally found in free-spawning marine invertebrates (FRANZÉN, 1970).

With the exception of the testis, the morphology of the unenclosed males and hermaphrodites is as described by NARCHI (1969) for female *Pseudopythina rugifera*.

DISCUSSION

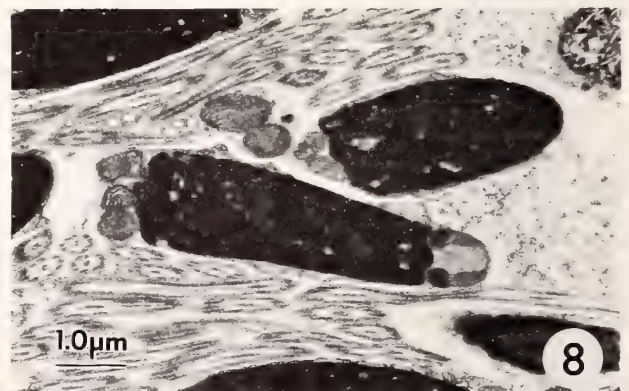
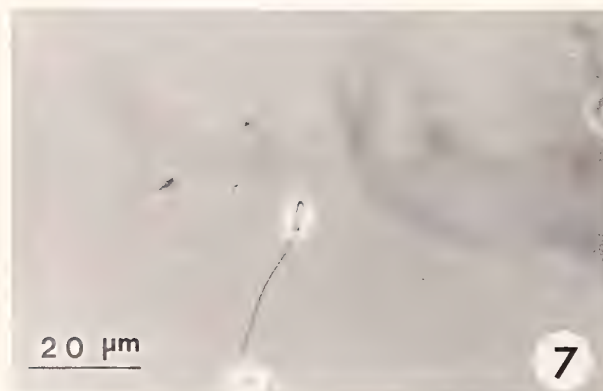
The Galeommatacea display various degrees of shell reduction and mid-mantle fold hypertrophy, associated with the development of a commensal habit (MORTON, 1976). *Pseudopythina rugifera* shows a strong dimorphism in this regard. Females and unenclosed males have a well-devel-

oped shell and an unspecialized mantle (NARCHI, 1969; personal observation), while the dwarf male shell is reduced and the mid-mantle fold enlarged. This may reflect the relatively protected environment of the endocommensal dwarf male within the female mantle cavity.

Additional morphological differences occur in the gills and foot. In female and unenclosed male *Pseudopythina rugifera*, the outer demibranch is present but is reduced in size relative to the inner demibranch (NARCHI, 1969). The lack of an outer demibranch in dwarf males may be a consequence of their small size, because juvenile eulamelibranch bivalves possess only one demibranch during their early development (STASEK, 1962). Foot morphology varies markedly between dwarf males and females or unenclosed males. The dorsoventrally compressed, suckerlike form of the dwarf male foot contrasts with the laterally compressed, slender foot of females and unenclosed males (NARCHI, 1969; personal observation). Females and unenclosed males attach to the ventral surface of *Aphrodita* by means of a large byssus (NARCHI, 1969; personal observation). Dwarf males also attach by byssus production, but, when moving around the female mantle cavity, they may rely for adhesion on the large area of surface-to-surface contact provided by the flattened foot.

The ciliated papillae present on the mid-mantle fold extension resemble the mechanoreceptors of the septibranch *Cardiomya planetica* (Dall, 1908) as described by REID & CROSBY (1980).

More than one dwarf male may locate in a single female *Pseudopythina rugifera*, as was reported by JENNER & MCCRARY (1968) for *Montacuta percompressa* and by MORTON (1976) for *Ephippodonta oedipus*. In these cases, the male spawning the largest amount of sperm coinciding with egg release should fertilize the greatest number of eggs. This would select for rapid sexual maturity in these dwarf males, as appears to occur in *P. rugifera*.



Explanation of Figures 7 and 8

Figure 7. Phase contrast light micrograph of *Pseudopythina rugifera* sperm.

Figure 8. Transmission electron micrograph of *Pseudopythina rugifera* sperm.

NARCHI (1969) reported that in *Pseudopythina rugifera* the embryos develop within the gills, but he did not discover at what stage they are released. Commensal galeommataceans, with the exception of *Montacuta phascolionis*, undergo a planktotrophic developmental stage (OCKELMANN & MUUS, 1978). *Montacuta phascolionis* has direct development with a maximum fecundity of circa 73 embryos (GAGE, 1979). Based on the relatively high fecundity (thousands of embryos) of *P. rugifera* (personal observation), direct development is unlikely.

In the Galeommatacea, dwarf male morphology varies from the extreme degeneration of *Montacuta percompressa* (JENNER & MCCRARY, 1968), to *Ephippodonta oedipus*, where the dwarf male is simply smaller than the female (MORTON, 1976). Secondary sexual characteristics are moderately well developed in the other species with dwarf males. The dwarf males of *Oorbitella floridana* and an undescribed *Entovalva* species are similar to *Pseudopythina rugifera* in that they are shelled and possess an enlarged foot (JENNER & MCCRARY, 1968).

Pseudopythina subsinuata is a protandric, consecutive hermaphrodite. The males frequently attach to the byssus of the larger females, and when very small occasionally occur within the mantle cavity of females (MORTON, 1972). Morton interpreted the *P. subsinuata* life cycle as an initial dwarf male phase followed by a female phase. The situation in *Pseudopythina rugifera* appears similar, with a smaller male stage being linked to a larger female stage by a period of simultaneous hermaphroditism (Figure 1). The initial (dwarf) male phase locates inside the female mantle cavity, and sex reversal occurs external to the female host. However, the role of the dwarf male stage may differ in these two species. MORTON (1972) implies that male *Pseudopythina rugifera* do not normally occur within the female mantle cavity. Furthermore, sperm transfer (presumably from unenclosed males) in *P. subsinuata* involves a storage of sperm morulae or ripe sperm in the suprabranchial chamber of females (MORTON, 1972). Sexually mature male *P. rugifera* typically reside within females, and the presence of spawned-out males occurring inside newly spawned females suggests that the dwarf male stage is largely responsible for sperm transfer in this species. It is not known whether sperm storage in the female suprabranchial chamber occurs in female *P. rugifera*. MORTON (1976) suggests that dwarf males in *P. subsinuata* evolved as a result of extreme protandry. Dwarf males in *P. rugifera* may have evolved similarly.

Available information suggests that all galeommatacean species may brood developing embryos in the suprabranchial cavity and/or the mantle cavity. The eggs are released into and fertilized in the suprabranchial chamber (BOOTH, 1979; CHANLEY & CHANLEY, 1970, 1980; LEBOUR, 1938; MORTON, 1972; NARCHI, 1969; OCKELMANN & MUUS, 1978; Ó FOIGHIL & GIBSON, 1984; OLDFIELD, 1964; PÉRÈS, 1937). TURNER & YAKOVLEV (1983) describe a similar situation in the teredinid *Zachsisia zenkewitschi* and propose that the presence of dwarf males in

Table 1

Methods of bulk sperm transfer in galeommatacean bivalves.

Species	Method of sperm transfer
<i>Montacuta substriata</i> (Montagu, 1808)	enclosed in "nutritive cells" (OLDFIELD, 1961)
<i>Montacuta</i> (<i>Tellimya</i>) <i>ferruginosa</i> (Montagu, 1808)	enclosed in "nutritive cells" (OLDFIELD, 1961)
<i>Mysella bidentata</i> (Montagu, 1803)	spermatophores (DEROUX, 1961)
<i>Pythinella cuneata</i> (Verrill & Bush, 1898)	enclosed in "elongate sacs" (GAGE, 1968)
<i>Pseudopythina subsinuata</i>	sperm morulae (MORTON, 1972)
<i>Entovalva perrieri</i> (Malard, 1903)	spermatophores (personal observation)
<i>Mysella tumida</i> (Carpenter, 1864)	spermatophores (personal observation)
<i>Potidoma clarkiae</i> (Clark, 1852)	spermatophores (personal observation)
<i>Oorbitella floridana</i>	dwarf males (JENNER & MCCRARY, 1967)
<i>Montacuta percompressa</i>	dwarf males (JENNER & MCCRARY, 1967)
<i>Entovalva</i> sp.	dwarf males (JENNER & MCCRARY, 1967)
<i>Ephippodonta oedipus</i>	dwarf males (MORTON, 1976)
<i>Pseudopythina rugifera</i>	temporary dwarf males (personal observation)
<i>Chlamydoconcha orcutti</i>	temporary complemental males? (MORTON, 1981)
<i>Montacuta phascolionis</i>	complemental males? (DEROUX, 1960)

this species leads to a high percentage of the eggs being fertilized. Likewise, dwarf males in *Pseudopythina rugifera* and other galeommatacean species may optimize fertilization success by getting sperm in large numbers to the fertilization site.

An alternative method of bulk sperm transfer occurs in a number of commensal galeommatacean species. This usually entails the encapsulation of sperm masses within nutritive cells, membranous envelopes, or bags, usually called spermatophores (Table 1), which are subsequently found attached to the gills of a conspecific (OLDFIELD, 1961; OCKELMANN & MUUS, 1978; personal observation). Although the details of spermatophore transfer have not been revealed for most of these species, the spermatophores in *Mysella tumida* are released into the environment and taken back into the gill chamber, *via* the exhalant opening (personal observation.).

Although both spermatophores and dwarf males achieve sperm transfer between individuals, they differ in one important aspect—spermatophores have no inherent locomotory abilities and consequently are more restricted in their dispersal ability, probably to conspecifics occurring on the same host. Galeommatacean species with dwarf

males have a planktonic larval stage (CHANLEY & CHANLEY, 1970; MORTON, 1976) which, assuming some of the larvae to be potential dwarf males, would result in enhanced dispersal.

Spermatophores as a means of sperm transfer may be more efficient than dwarf males where space restrictions on or around the host does not normally prevent the co-occurrence of equal-sized adult commensals. This proposal is in accordance with ecological data provided by GAGE (1966) for *Montacuta substriata* and *Montacuta ferruginosa*, GAGE (1968) for *Pythinella cuneata*, OCKELMANN & MUUS (1978) for *Mysella bidentata*, and personal observations on *Mysella tumida*. A possible exception is *Entovalva perrieri*, where individuals have been recorded to occur singly on their holothurian hosts (POPHAM, 1940).

Commensal galeommataceans with dwarf males occur attached to the host (JENNER & MCCRARY, 1968; CHANLEY & CHANLEY, 1970; DALL, 1899), or in the case of the *Entovalva* sp., in the tubes of the polychaete host (ABBOTT, 1974). Where space restrictions on or around the host species may normally prevent the co-occurrence of equal-sized adult commensals, and host distributions are discrete, the dwarf male method may be the more effective means through which sperm transfer is achieved. This condition seems to be developing in *Pseudopythina subsinuata*, where the animals are restricted to a very specific location, the last thoracic and first abdominal segments of their stomatopod crustacean hosts (MORTON, 1972). Stomatopods are considered to be territorial with non-overlapping distributions (BROOKS, 1965). A similar situation may exist when *P. rugifera* occurs on *Upogebia pugettensis*. The location of *P. rugifera* on this host is also very restricted (DALL, 1899; MORTON, 1972), and laboratory observations suggest that *U. pugettensis* is territorial (personal observation).

Pseudopythina rugifera also occurs as an ectocommensal on the polychaete *Aphrodita* (MACGINITIE & MACGINITIE, 1968). Space restrictions on this host are not as severe as on *Upogebia pugettensis*, and up to 13 specimens may attach to one *Aphrodita* (personal observation). It may be that *U. pugettensis* is the original host species for *P. rugifera* and that dwarf males were evolved before *Aphrodita* also became a host.

Differences in the two sperm transfer methods are not absolute, as is best shown by *Pseudopythina subsinuata*. Here, although a temporary dwarf male phase exists, the males may be separate from the females and sperm are transferred as morulae to the gills of the female (MORTON, 1972).

As mentioned in the Introduction, the dwarf males reported by MORTON (1981) for *Chlamydoconcha orcutti* and by DEROUX (1960) for *Montacuta phascolionis* occur in association with larger, hermaphroditic individuals, and may perhaps be better classified as complementary males. This term refers to small males living in association with large, hermaphroditic conspecifics. Use of this term implies that these males are inherently incapable of devel-

oping into hermaphrodites (HUI & MOYSE, 1984). It is not clear whether the *M. phascolionis* are strictly complementary, or are individuals that switch from the male condition to simultaneous hermaphroditism as suggested by JENNER & MCCRARY (1967). MORTON (1981) suggests that, based on the structure of male and hermaphroditic valves, the miniature males of *C. orcutti* eventually become free-living and hermaphroditic.

Whatever the ultimate fate of the males in *Montacuta phascolionis* and *Chlamydoconcha orcutti*, they are complementary in function while they exist as males. The hermaphroditic individuals may presumably outcross with either the males or with other hermaphrodites. This situation would appear to combine the advantages of both the dwarf male condition and spermatophore exchange between equal-sized hermaphroditic adults, thus facilitating outcrossing in habitats with or without space restrictions. Complementary males, however, may face competition in transferring sperm to the host hermaphrodite from neighboring hermaphrodites (CRISP, 1983). Dwarf males only compete with each other in this respect. This suggests that dwarf males are more stable over time than complementary males.

CRISP (1983) proposes that dwarf males in the barnacle *Ibla cumingii* (Ranzani) evolved by way of a complementary male stage. Figure 9 depicts a hypothetical scheme outlining how a similar evolutionary pathway may have occurred in the Galeommatacea, as a result of adaptation to physically restricted habitats. In this scheme, condition A is that of an outcrossing hermaphroditic species, where the testis initiates development earlier than the ovary. This hypothetical species occupies a diverse range of habitats, including some where space restrictions may occur. BAREL & KRAMERS (1977), OCKELMANN & MUUS (1978), and Ó FOIGHIL *et al.* (1984) describe essentially this situation for *Mysella bidentata*. If over time, the species becomes specialized for physically restrictive habitats, the mean number of small individuals (predominantly male) per site will increase relative to the number of larger hermaphrodites. Sperm transfer will increasingly be carried out by the small males, which become complementary in function (condition B). *Montacuta phascolionis*, as described by PÉRÈS (1937) and DEROUX (1960) seems an appropriate example. Complementary males have an additional reproductive advantage over the larger hermaphrodites in the relatively short amount of time required to achieve sexual maturity (CRISP, 1983). In *M. phascolionis*, the proportion of testis to ovary in the hermaphroditic gonad is much reduced relative to that of other *Montacuta* species (DEROUX, 1960). Hermaphroditic individuals of barnacle species with complementary males show a similar reduction in the size of the testis, due to the lower reproductive fitness of the male function in the hermaphrodite (CRISP, 1983). This trend should continue as habitats become yet more restricted, until all sperm transfer is carried out by the small males, and the larger individuals are female in function (condition C). *Pseudopythina rugifera* belongs to

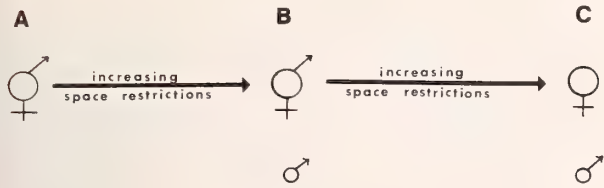


Figure 9

Hypothetical scheme for the indirect evolution of dwarf males in the Galeommatacea by way of a complementary male stage. A, hermaphrodites only; B, hermaphrodites and complementary males; C, females and dwarf males.

this, the dwarf male category. Alternatively, as mentioned above, dwarf males may evolve directly under similar environmental conditions, as a result of extreme protandry (MORTON, 1976).

The evolution of complex reproductive cycles in galeommataceans was a prerequisite for the successful adoption of a commensal mode of life (MORTON, 1976). An important step was the development of efficient modes of sperm transfer (OCKELMANN & MUUS, 1978). In some species, including *Pseudopythina rugifera*, this involves the use of dwarf males. Through the medium of dwarf males, gene exchange may be facilitated between individuals that are widely separated as a result of the space restrictions and distribution patterns of their habitats. A more detailed knowledge of the reproductive cycles and ecology of the relevant species is needed to increase our comprehension of the reproductive significance of dwarf males, spermatophores, and suspected complementary males in the Galeommatacea.

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Life-habits and Infaunal Posture of *Cumingia tellinoides* (Tellinacea, Semelidae): An Example of Evolutionary Parallelism

by

W. D. RUSSELL-HUNTER AND JAY S. TASHIRO¹

Marine Biological Laboratory, Woods Hole, Massachusetts 02543, and
Department of Biology, Syracuse University, Syracuse, New York 13210

Abstract. The semelid clam *Cumingia tellinoides* is an infaunal burrowing form found in sandy organic deposits. Its eggs have been used in experimental embryology for over 80 years, and it has usually been reported to have a vertical life-posture and a "nearly equivalve" shell. In populations from the Cape Cod area, the majority of individuals live and feed while lying horizontally within the sediment and show asymmetries of shell structure. Observations and photographs of movements and feeding postures were made possible by use of artificial substrates prepared from cryolite.

There is considerable individual plasticity of behavior and shell variation in *Cumingia tellinoides*. For all field and laboratory observations, 76.1% of individual clams were found lying on one shell valve (and in 78.4% of these it was the left valve down). Some corresponding deformation of the posterior shell margins was found in 79.2%, and in 42.9% this amounted to a clear lateral twist (in 65.4% of these to the right, or posturally upwards). Internal asymmetries of the pallial sinus were found in 60.8% of shell valve pairs, and there was a significant ($P < 0.05$) inverse correlation between lateral twist direction and larger sinus scar areas in *Cumingia tellinoides*. In contrast, in the sympatric tellinid clam *Macoma tenta*, all were found lying on their left valves, all shells showed a right-handed twist, and 93.7% had a larger area in the left pallial sinus.

The pattern of horizontal feeding posture, associated with posterior twisting and asymmetric pallial lines in the shell valves, appears to be variably expressed in *Cumingia tellinoides*, contrasting with similar but obligate features in *Macoma tenta*. It seems most probable that the occurrences of horizontal life-style (and associated asymmetries of shell and muscles) in both semelid and tellinid lineages constitute an example of evolutionary parallelism rather than of evolutionary convergence.

INTRODUCTION

LITTLE HAS BEEN published on the natural history of the semelid clam *Cumingia tellinoides* Conrad despite extensive laboratory use of its eggs as material for experimental embryology for over 80 years. In general, within the burrowing and infaunal superfamilies of lamellibranchs, an inequivalve condition of the bivalve shell is associated with a non-vertical posture in the substrate. More than half of the species in the Tellinidae, and a number of species in the Semelidae, are known to have a twist (usually to the

right) of the posterior margins of their shell valves. Earlier surveys of the life-habitats of such infaunal bivalves (STANLEY, 1970; ABBOTT, 1974) claimed a vertical life-posture and a "nearly equivalve" shell for *Cumingia*.

We now report that, in *Cumingia tellinoides*, the majority of individuals live and feed while buried nearly horizontally in the sediment, and many show not only a slight posterior twist to the shell valves but also an internal asymmetry of the scars of the pallial sinus (that is, of the attachment of the siphonal retractor muscles to the shell valves). Use of artificial deposits made from the pure mineral cryolite allowed us to obtain photographs of living specimens of *C. tellinoides* in their feeding posture within the substrate (some reproduced here). These observations and results are discussed in relation to other molluscan

¹ Present address: Department of Biology, Kenyon College, Gambier, Ohio 43022.

examples of parallelism and convergence in adaptation. Critical assessment of cladistic systematics has re-emphasized the need for discrimination between convergence and parallelism (MAYR, 1974), and this is partly responsible for a revival of interest in such evolutionary distinctions at all levels of biological organization.

MATERIALS AND METHODS

In the Cape Cod area, *Cumingia tellinoides* lives in sandy organic deposits associated with eelgrass (*Zostera*), around the level of MLWST and for about 20 cm deeper. More specifically, it is found in fine sand with a high fraction of peaty material and sometimes even among eelgrass roots, not usually under the densest beds of *Zostera*, but rather where there are sparser clumps of eelgrass along the margins of the little channels that drain the flats during the lowest tides (GRAVE, 1927; and author's observations). Healthy specimens used for measurement and photography were collected on various occasions between 1973 and 1981 from an area of flats in the Northwest Gutter of Hadley Harbor (in the Elizabeth Islands, near Woods Hole). Populations of *C. tellinoides* have also been examined in the other gutters of the Hadley system, and in similar microhabitats in the tidal harbors of North Falmouth, Quisset and Orleans, all on Cape Cod. From about 1907 to 1927, *C. tellinoides* was collected regularly and intensively to provide eggs for embryologists and cell-physiologists (including H. E. Jordan, E. G. Conklin, F. R. Lillie, E. Browne-Harvey, B. H. Grave, T. H. Morgan, and L. V. Heilbrunn) working in the Marine Biological Laboratory at Woods Hole. It apparently became a very rare species with the decline of eelgrass beds between 1930 and 1960, but was listed normally and not marked as "rare" in a faunal key prepared in 1963 (RUSSELL HUNTER & BROWN, 1964). It is now (1980-83) not uncommon again, although limited to certain localities and to the highly specific microhabitat described above.

The family Semelidae, in which the genus *Cumingia* is placed along with *Semele* and *Abra*, can be separated from the family Tellinidae (including *Tellina* and *Macoma*) by major differences in the functional shell ligament and in hinge dentition. These features of shell morphology will be discussed more fully below, but it should be noted that *Cumingia* (like all semelids) has an internal resilium (carried on a chondrophore plate) as its functional shell ligament, while all tellinids, including those local species of *Macoma* which can be nearly sympatric (*Macoma tenta* and *M. balthica*), have elongate external ligaments.

Observations and photographs of the movements and feeding posture of *Cumingia tellinoides* within the substrate were made using artificial deposits ground and sieved to size from large pure crystals of the mineral cryolite, which has a refractive index close to that of seawater. Biological application of this material was first described by JOSEPHSON & FLESSA (1971, 1972), and its use for

these studies on *Cumingia* reported in an abstract (RUSSELL-HUNTER & TASHIRO, 1973). Cryolite media are better suited for invertebrates such as *Cumingia* that live in sand deposits, being more resistant to penetration than are those prepared from methylcellulose (HUNTER, 1982; HUNTER *et al.*, 1983) which are better for worms from flocculent mud deposits. When suitably illuminated, granular cryolite in seawater is relatively "transparent," permitting close observations of pedal and siphonal movements within the substrate and allowing photography at moderately high resolution.

Each experimental aquarium was prepared by clamping two sheets of plate glass (approximately 20 cm square) around a piece of thick-walled rubber hose (of 1.5 or 2.8 cm outside diameter) bent into a U-shape, and filling the U to a depth of 8 to 10 cm with field-collected natural substrate or with ground cryolite in about 15 cm of seawater. Photographs were taken with a 105-mm lens and bellows on a Bronica (6 cm square) camera, using Kodak Plus-X film rated at ASA 210 and developed in half-strength Acufine. Most photographs were taken with both front (direct) and back (transmitted) lighting of the substrate. The results (see Figures 1, 4, 6) show edge definition and resolution somewhat better than those achieved using X-radiography by STANLEY (1970) in the course of his heroic survey of the life habits of 98 extant bivalve species.

OBSERVATIONS AND RESULTS

During the summers from 1961 to 1972, the frequency with which *Cumingia tellinoides* appeared in field collections of the Invertebrate Zoology course at Woods Hole increased. In 1967 and 1968, casual inspection of samples totaling about 25 animals each year revealed that the majority showed some deformation of the posterior margins of the shell valves, with many showing a definite posterior twist as in Figure 3. Casual observations of live *C. tellinoides* in the same two years showed that the majority lay on one side in the sediment as did the more abundant *Macoma tenta*.

There is obviously some individual plasticity of behavior in *Cumingia tellinoides*. During a more intensive study in 1973, in the course of several burrowing experiments, a total of 51 specimens was left each for just over 48 h in dishes with about 6 cm depth of natural sediments freshly collected from the field. To describe orientation, we can use the sagittal plane of each individual clam (that is, the plane defined by both the antero-posterior and dorso-ventral axes which, in symmetrical bivalves, is also the plane where the edges of the shell valves meet on adduction). Of the 51, 7 (13.7%) had their sagittal planes vertical and thus could be actively burrowing, while 5 (10%) had their sagittal planes at about 45° to the surface of the sediment. The majority (39/51 or 76.5%) lay with their sagittal planes nearly horizontal (that is, parallel to the sediment surface). Shell-lengths of this group ranged from

9.0 to 17.8 mm (mean 12.6 mm) and, for those lying horizontal in the sediment, the average depth of burial was about 15 mm or just over one shell-length. In the field, living specimens of *C. tellinoides* are usually found buried at depths of about twice their individual shell-lengths. For 16 specimens carefully uncovered by finger in the field, none had vertical sagittal planes, and only 4 approached 45° from the horizontal. Both in the laboratory dishes and in the field, most horizontal specimens of *C. tellinoides* lay on their left side, but a few lay on their right (see shell proportions below). This contrasts with conditions in adjacent populations of the tellinid *Macoma tenta* where the feeding posture of every individual is lying on its left valve (which is somewhat more convex).

Many tellinids, which take up a horizontal feeding posture within the substrate, burrow relatively rapidly from the surface with their sagittal planes at a low angle from the horizontal (HOLME, 1961; STANLEY, 1970). For each species studied in detail, an obligate orientation has been reported. In contrast, individuals of *Cumingia tellinoides* burrow rather slowly, and enter both natural sediments and cryolite deposits with their sagittal planes at a slight angle to the vertical (Figures 1, 2). The dorsal or hinge side is characteristically lower, but the slight lateral inclination that is normal may be to either the left or the right side. Burrowing is essentially similar to that in unspecialized and more globose bivalves (ANSELL & TRUEMAN, 1967; TRUEMAN, 1968; TRUEMAN *et al.*, 1966), with alternate *points d'appui* being provided by the opening gape of the shell valves and the dilatible foot. Some feeding can go on during parts of the burrowing cycle (Figure 1). At a depth corresponding to shell length, the lateral inclination increases and the sedentary posture (nearly horizontal) is taken up. Figures 4, 5, and 6 show specimens with siphons extended for feeding. Once this posture is established the foot is rarely extended, and it is likely that, in the peaty sand substrates of the field, *C. tellinoides* does not move much once established in the substrate. A number of earlier authors including STANLEY (1970) have claimed a vertical posture for *C. tellinoides* when feeding, and one X-radiograph in his survey shows four specimens all anterior down and vertical with siphons extended in feeding, with channels in the substrate revealing former positions. It seems possible that the individual plasticity of behavior (including infaunal posture) in *C. tellinoides* could involve different norms for different populations, perhaps with some relation to different substrate conditions.

In all of our observations (including the clams of Figures 4, 5, and 6) the inhalant (ventral) siphon was directed nearly vertically and was used in both suspension and deposit-feeding, while the exhalant (dorsal) siphon discharged below the surface or reached it at an obtuse angle at least 10 mm away from the inhalant. With healthy animals in cryolite deposits, it is easy to distinguish the small spherical fecal pellets and the larger, somewhat less consolidated, masses of pseudofeces as they move within

the extended siphons. Only true feces are discharged through the exhalant siphon, they pass slowly but regularly into the substrate, either (Figure 4) close to the dorso-posterior shell margin with little siphonal extension, or (Figures 5, 6) in a wide arc posteriorly and upward. Similar discharge of the exhalant siphon within the substrate has been reported for the tellinids *Macoma nasuta* (MACGINITIE, 1935) and *Arcopagia crassa* (HOLME, 1961). At irregular intervals the larger softer masses of pseudofeces are shot vertically up the inhalant siphon high above the sediment surface (as a result of partial valve adduction). [It should be noted that, in Figure 4, a fecal pellet shown halfway to the surface is *not* inside the inhalant siphon.] More frequent discharge of pseudofeces (in somewhat larger, looser masses) occurs during periods of deposit-feeding. This flexibility of feeding behavior found in *Cumingia tellinoides* is probably unusual in semelid and tellinid bivalves since most investigators (YONGE, 1949; HOLME, 1961; STANLEY, 1970; ABBOTT, 1974) suggest that each species in these two families is either a suspension feeder or a deposit-feeder. However, BRAFIELD & NEWELL (1961) have claimed that certain British populations of *Macoma balthica* show tidally controlled alternation of suspension- and deposit-feeding. For the same species in Denmark, RASMUSSEN (1973) has illustrated both feeding modes. However, GILBERT (1977) regards it as an obligatory deposit feeder, while TUNNICLIFFE & RISK (1977) conclude that it must supplement its protein intake by suspension-feeding when submerged.

Figure 7 is a vertical photograph of the inhalant siphon of a specimen of *Cumingia tellinoides* living in natural substrate and engaged in deposit-feeding. Despite the quality of the photograph (poor contrast, and little depth of focus), some radiating marks can be detected on the surface of the sediment. These are in conformity with our observations that, during deposit-feeding the recurved inhalant siphon of *C. tellinoides* is not swept in a circular path as is the case in most deposit-feeding tellinids (YONGE, 1949; HOLME, 1950, 1961; STANLEY, 1970), but sucks in a series of radial skimming movements directed centripetally (like *Macoma tenta*; STANLEY, 1970). Rejection of pseudofeces commonly occurs after each group of three or four radial sweeps.

Three collections of *Cumingia tellinoides* totaling 79 individuals were used to quantify shell variation. Most of these were killed by immersion in hot water and subsequent removal of the soft tissues, but 17 clams had initially been fixed in formalin. Of the total, 2 were damaged in preparation and 3 others were too small for assessment of the pallial sinus, so that shell features are reported for 77 shell-valve pairs (or 74 pairs for sinus asymmetries). Some deformation of the posterior part of the shell was found in one or both valves of 61/77 or 79.2%, and this amounted to a clear twist (as in Figure 3) in 33/77 or 42.9%. In a few cases, a twist to the left had been preceded by a twist to the right, or vice versa, and in two sets of valve pairs a series of alternate "twists" seemed to have oc-

curred. Of these with a single clear twist, 9/26 turned left while 17/26 turned right. This figure of 65.4% with the posterior shell margins turned right (corresponding to growth during a sedentary period of infaunal posture lying on the left valve) is considerably less than the figure of 78.4% for clams found alive lying on their left valves (as a percentage of the combined numbers for all live field and laboratory observations found lying horizontally, which amounted in turn to 76.1% of all observations). In other words, although left valve down occurs in a majority (59.7%) of our live observations, the corresponding shell twist is found only in a plurality (22% single clear, or 28.6% total) of shell pairs studied.

Another asymmetry shown by the shell-valve pairs, which may be of considerable functional importance, concerns modification of the internal attachment of the siphonal retractor muscles. These so-called pallial sinus scars form embayments of the pallial lines, which elsewhere run concentric with the shell margins and mark the insertion in the nacreous layer of the shell for the line of muscles from the innermost of the three lobes of the mantle edge. Asymmetries between left and right shell-valves of the pallial sinus scars can involve (a) the areas enclosed by the scars (reflecting the "spread" of the muscle attachments), (b) the width of the scar lines (reflecting the thickness of the attached muscle sheet), or (c) the shape of the sinus embayment ranging from broadly ovate to triangular. This third kind of asymmetry is less easily quantified. One or more of these three asymmetries were found in 45/74 or 60.8% of the shell-valve pairs. Once again there were biases of orientation but no uniformity of handedness. The scar area was larger in 19 left valves and in 14 right valves, and the scar was more pronounced in 8 left valves and in 14 right valves. There was a tendency for

those shells with the posterior margins twisted to the right (being the plurality) to show larger scar areas in the left valve and more pronounced scar lines in the right valve, while the shells with a left-handed twist (the minority) tended to show the opposite conditions. In a 3×3 contingency table, there was a significant inverse correlation between marginal twist direction and larger sinus scar areas (summed chi-squares = 10.667, df 4, $P < 0.05$). For comparison, in a sample of *Macoma tenta* totaling 63 individuals, all shells showed a right-handed twist which could involve more than one third of the length of the shell, and 59/63 or 93.7% showed a larger pallial sinus area in the left valve. Clearly in *Cumingia tellinoides* those shell asymmetries related to infaunal posture show levels of individual variation that parallel the individual plasticity of behavior.

DISCUSSION

The fact that *Cumingia tellinoides* is found in a marginal microhabitat is relevant to any discussion of the variable behavior exhibited by individuals and of the related asymmetries of their shells.

Two principal life-styles are found in the bivalve sub-order or superfamily Tellinacea. Some species and genera show a capacity for rapid reburrowing associated with symmetrical, streamlined, smooth shells, and those may live in shifting substrata or move laterally in a near horizontal orientation in the course of deposit-feeding (HOLME, 1961; STANLEY, 1970). Other, often closely related, species are less typically members of the mobile "superficial in-fauna," seem adapted for a more permanently sedentary way of life, and may live in peaty deposits or among the root systems of eelgrass (*Zostera*) or turtle-grass (*Thalas-*

Explanation of Figures 1 to 7

Figure 1. An early stage in burrowing in an adult specimen of *Cumingia tellinoides* (12.8 mm shell length), with some feeding continuing through the open siphons. The photograph was made in an artificial deposit of ground and sieved crystalline cryolite (as were Figures 2, 4, 5, and 6).

Figure 2. The same clam as in Figure 1 a few seconds later, with the dilatable foot being extended and the siphons closed.

Figure 3. Dorsal view of the posterior margins in an adult shell of *Cumingia tellinoides*. The right shell valve is above, and the scale-bar equals 1 mm.

Figure 4. Sedentary feeding posture of an adult specimen of *Cumingia tellinoides* (13.3 mm), photographed in cryolite with the dorsal (hinge) side toward the camera, showing the inhalant siphon extending vertically to the surface. [Note that the fecal pellet halfway to the surface is *not* inside the siphon.]

Figure 5. Feeding posture in another (11.9 mm) specimen viewed from the ventral side. Three fecal pellets have been deposited by the downturned exhalant siphon close to the posterior shell margin.

Figure 6. Ventral view of the feeding posture in another (14.6 mm) specimen. This clam is engaged in suspension-feeding rather than deposit-feeding. Fecal pellets have been deposited in an arc up to the surface of the deposit by the exhalant siphon which is extended horizontally in the photograph.

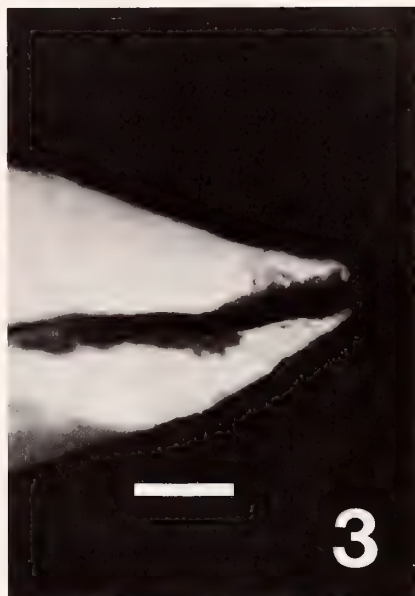
Figure 7. Vertical photograph of the inhalant siphon of a specimen of *Cumingia tellinoides* living in natural substrate. The faint radial marks to the right of the siphon represent tracks of recent inhalant passes during deposit-feeding. The scale-bar equals 2 mm.



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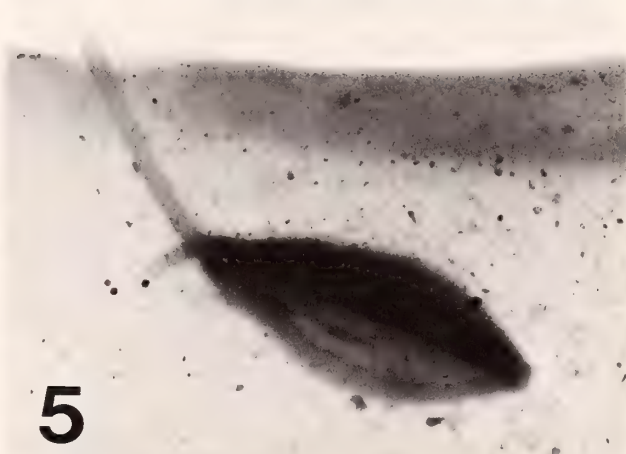
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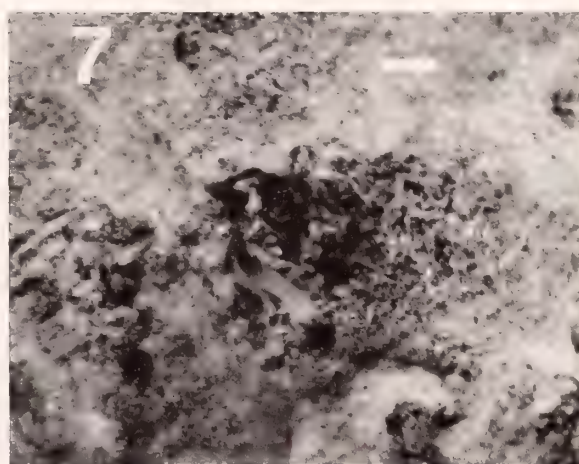
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sia). Despite statements by some authors, there is no universal correlation of the first life-style with deposit-feeding and the second with suspension-feeding. Asymmetries of the shell valves of adults (including the posterior marginal twist, and inequalities of the pallial sinus) are clearly associated with a horizontal infaunal habit (*i.e.*, lying on one shell valve), and increased functional efficiency in that posture. However, it now appears that either life-style (rapid-reburrowing or sedentary) may be associated with a horizontal infaunal posture. Further, the results from this study of *Cumingia tellinoides* demonstrate that great individual shell variation and plasticity of behavior are possible within a species.

Features common to the four families of the Tellinacea include separate long extensible siphons, a blade-like foot for burrowing, a pallial cruciform muscle (GRAHAM, 1934; YONGE, 1949, 1957), and rather large labial palps. During deposit-feeding, the palps are used for sorting the detritus which is sucked in from the surface by a vacuum-cleaner-like action of the inhalant siphon (Figure 7). Within the superfamily, two of the families, the Tellinidae, to which the genera *Tellina* and *Macoma* belong, and the Semelidae, to which *Semele*, *Abra*, and *Cumingia* belong, can be separated by major differences of the functional ligament and hinge dentition. The tellinids have an elongate external ligament with rather weak teeth, while the semelids have an internal resilium as the functional ligament (carried on a chondrophore plate rather like that of *Mya*), and strong cardinal and lateral hinge-teeth. These are features regarded as phylogenetically sound and as genetically conservative by most systematists and paleontologists. This assessment need not be modified by the observations of TRUEMAN (1953, 1966) which suggest that the larger internal ligament of the semelids is homologous with the tiny cardinal ligament present temporarily in juveniles (spat) of some tellinids (*Macoma* and *Tellina*), and is therefore neotenic.

Cumingia tellinoides is frequently found living with *Macoma tenta* (although *M. tenta* is more widely found alone in bare muddy sands 3–8 m below MLWST). The habit of lying on one side in the sediment (as done by both species) and the structural asymmetries associated with the habit, must have evolved independently in semelids and tellinids. There are a number of other well-established cases of ecologically sympatric pairs of species derived from morphologically distinct stocks of bivalves. As discussed by MAYR (1969, 1974) and BOCK (1963, 1965) it is often difficult to distinguish cases of major evolutionary convergence from similarities in allied stocks which result from parallelism. Among bivalves, striking similarities of shell structure and muscle mechanics can be found in sympatric forms derived from widely different superfamilies—for example, fused-siphon deep-burrowers from both Myacea and Mactracea, globose ribbed cockles from Cardiacea and Arcacea, and borers in soft rock (*Hiatella*, *Petricola*, and *Zirphaea*) from three distinct superfamilies. These are almost certainly all cases of evolutionary con-

vergence as distinguished by MAYR (1969, 1974), as are the many and polyphyletic stocks of limpetlike gastropods (RUSSELL-HUNTER, 1982).

With the common features of infaunal posture and shell modification in *Macoma* and *Cumingia*, however, we may be observing the results of parallelism, or similarities of structure and function produced by shared genotypic features (not expressed in this combination in other related forms). In this view, some of the other features noted above as common to the overall group, the Tellinacea, are of paramount importance. These include the cruciform muscle (YONGE, 1949, 1957; see also GRAHAM, 1934), which may be involved in adjusting the basal attitude of the siphons, and also the mode of extension of the siphons (CHAPMAN & NEWELL, 1956; see also CHAPMAN, 1958) using radial muscles *within* the siphonal walls, so that water circulation and feeding can go on during a smooth and continuous process of protrusion. This is totally unlike the mechanism of siphonal extension employed in *Hiatella* (RUSSELL HUNTER, 1949) and in *Mya* (CHAPMAN & NEWELL, 1956) where protrusion occurs in step-wise stages involving *closed* siphonal tips and serial contractions of the shell adductor muscles. Along with these features common to the shared superfamily, the tellinid *Macoma* and the semelid *Cumingia* both exhibit structural features, such as the posterior shell twist and asymmetries of the pallial sinus, which may be correlates of a horizontal infaunal posture. Evolutionary hypotheses regarding such correlates must be based on analyses of function, and of adaptive significance, as clearly articulated by BOCK (1965, see also BOCK & VON WAHLERT, 1965) in discussing similar vertebrate cases. In considering all bivalve species in the Tellinacea (or all individuals in a variable species like *Cumingia tellinoides*), it is important to note that these correlates of structure with behavior are not reciprocal. All twisted shells occur in species (or individuals) that live in a horizontal infaunal posture, but not all forms living horizontally have shell twists.

The functional significance of the shell twist is clearly related to its molding of the siphonal bases and to the hydraulics of water circulation in feeding. MACGINITIE (1935) provided the earliest description of the implications of the horizontal posture for feeding behavior in *Macoma nasuta*, and this was built upon by HOLME (1961) in his observations on five British tellinid species with this life-style. It was left to STANLEY (1970) to illustrate and discuss the fact that an upward twist of the posterior valve margins (where the siphons emerge from the shell) serves to broaden the radius of siphonal curvature and streamline water flow. This can be seen in Figures 4 and 6, and it is obviously more important to the inhalant siphon with its near vertical orientation. Our observations on *Cumingia tellinoides* in cryolite confirm Stanley's functional analysis, but add the necessary discharge of pseudofeces through the *inhalant* siphon as a factor favoring streamlining of the bend in that siphon at the shell margin. As already noted, in the sympatric form *Macoma tenta* all individuals

lie horizontally on their left valves, and all show a right-handed posterior twist, which can extend over one-third of the length of the shell. [There is an intriguing possibility that mirror-image races of *M. tenta* may exist, because ABBOTT (1974) gives as specific characteristics "posterior and narrower end slightly twisted to the left."] However, unlike the variable conditions found in *C. tellinoides*, curvature of the shell in *M. tenta* is universal and seems to result from an obligate growth pattern which continues through most of adult life and results in the left valve being somewhat more convex than the right. This is carried even further in another bizarre tellinid, *Tellidora cristata*, which has an almost "oyster-like" arrangement of a flat left valve and a bowl-shaped right valve. Unfortunately, nothing is known about life-habits in *T. cristata*.

Two distinct life-styles have been associated with the horizontal infaunal posture. In active species like *Tellina tenuis* and *T. agilis*, HOLME (1961) and STANLEY (1970) claim that the horizontal posture facilitates lateral movements in the substrate within a single plane, thus maintaining an even depth of burial. In contrast, in some species of *Macoma* and in *Cumingia tellinoides* the horizontal posture is associated with more permanently immobile feeding habits and a relatively sedentary life-style. This is also the case for *Semele proficua*, which has a symmetrical discoid shell but lives horizontally on its left side among roots of *Thalassia*, and could also be predicted as the life-style of the extremely asymmetric *Tellidora*. To further complicate matters, several species of *Macoma* with marked asymmetry of the pallial sinus have no shell twist and have been listed in most general accounts (along with *C. tellinoides*) as having a vertical life posture and near equi-valve shells. General surveys of fossil faunas of bivalves show a majority of species to be infaunal (NICOL, 1968), and inequivalve representatives to occur in at least 28 families (NICOL, 1958; see also NEWELL & MERCHANT, 1939), but reveal no regularities of habit.

Given the variety of associations listed above for the Tellinacea, it seems most probable that the occurrences of horizontal life-style (and associated asymmetries of shell and muscles) in both tellinid and semelid lineages constitute an example of evolutionary parallelism. Although it makes no reference to shared genotypic features, an early definition by SIMPSON (1961) remains valid: "parallelism is the independent occurrence of similar changes in groups from a common ancestry and because they had a common ancestry." An earlier discussion of parallel adaptations in related stocks was set out by RENSCH (1943) along with other germinal ideas about evolution above the species level, and OSCHE (1965) gives more detailed analyses of the potentialities of "hidden" gene combinations. The importance of attempting to discriminate between evolutionary convergence and parallelism has been re-emphasized in the course of a critique of cladistic systematics (MAYR, 1974), and in relation to the debate on molluscan evidence for punctuated equilibria in evolutionary lineages (MAYR,

1982). The present example of parallelism provided by the pattern of variably expressed behavior and shell morphology in the semelid *Cumingia tellinoides*, and of similar but obligate features in the tellinid *Macoma tenta*, may permit future experimental investigation. Meanwhile, use of such features as asymmetry of the pallial sinus to deduce life-style or infaunal posture in stocks of fossil or extant bivalves is questionable.

ACKNOWLEDGMENTS

It is a pleasure to thank John J. Valois, the manager of the marine resources department of the Marine Biological Laboratory, who not only aided us with boat transport to Northwest Gutter, but later confirmed, from his wide knowledge of the distribution of invertebrates in Cape waters, both our summary of the history of local abundance of *Cumingia tellinoides* and our description of its microhabitat. We are also grateful to boat captain Dickson A. Smith for collecting the comparative population sample of *Macoma tenta*. We must again thank Perry Russell-Hunter for assistance with reference material, and Barbara J. Carns and Myra Russell-Hunter for help in the preparation of this paper. The work was partly supported by a faculty research award to Jay S. Tashiro from Kenyon College, and a research grant DEB-78-10190 from the National Science Foundation to W. D. Russell-Hunter.

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Patterns of Sex Change of the Protandric Patellacean Limpet *Lottia gigantea* (Mollusca: Gastropoda)

by

DAVID R. LINDBERG

Museum of Paleontology, University of California, Berkeley, California 94720

AND

WILLIAM G. WRIGHT

Scripps Institution of Oceanography, La Jolla, California 92093

Abstract. Experiments were done to test the effects of density and age on the probability of sex change in the protandrous limpet *Lottia gigantea* (Sowerby, 1834). Because of tag loss and mortality, final numbers of individuals in each experiment were low. However, some trends are present in these data that are distinctive. Young, territorially subordinate limpets, transplanted to large, isolated, empty territories, had a low proportion of sex changers during the first year of the experiment (4/22), but a significantly higher proportion during the second year (9/11). Limpets maintained at higher densities had a low proportion of sex changers during both the first (1/7) and second (1/5, 1/7, 1/12) years after transplantation, regardless of age. These data suggest that either low density promotes sex change with a one year lag period, or that high density inhibits sex change that would otherwise occur when the limpets are 2 to 3 years old. The presence of an inherent probability of sex change cannot be ruled out.

INTRODUCTION

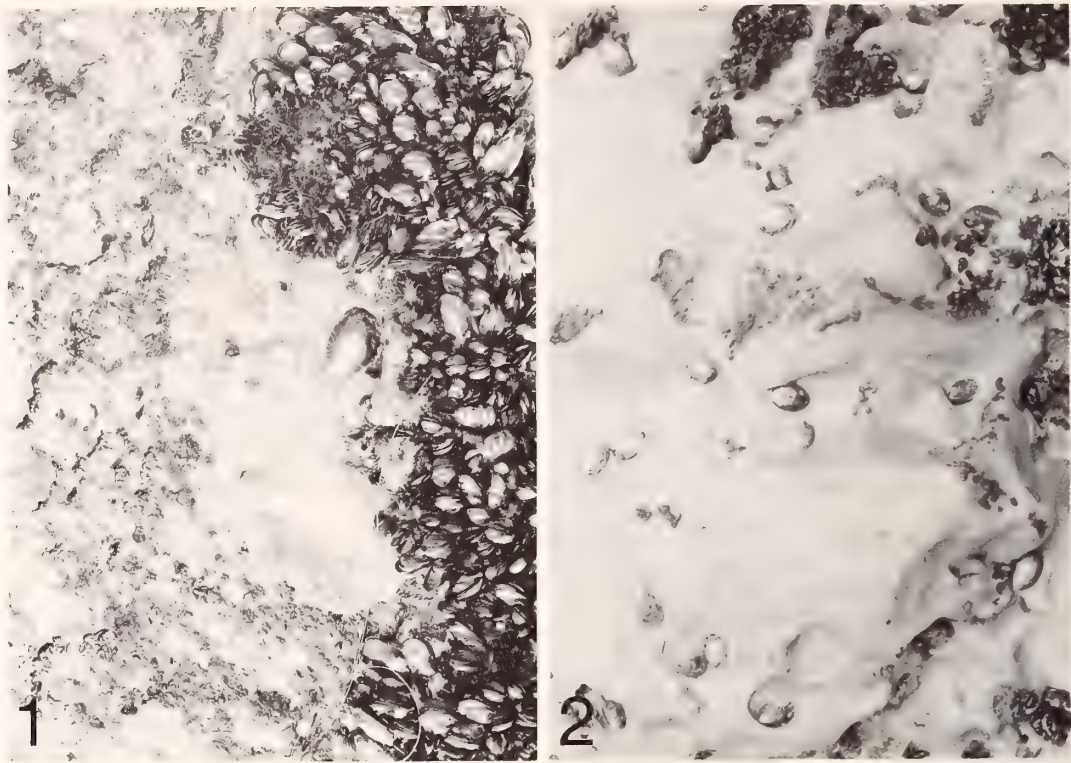
SEX-CHANGING MARINE invertebrates have received considerable attention over the last few years (see review by POLICANSKY, 1982). Most of the documented cases involve protandry (male → female) and several scenarios and models have been proposed to explain its selective advantage or adaptive significance (GHISELIN, 1974; WARNER, 1975; CHARNOV & BULL, 1977).

Protandry has often been investigated in the Mollusca, and occurs in a diverse group of taxa within the phylum (POLICANSKY, 1982). Taxa with copulatory structures are usually the subjects of these investigations because changes in sex are readily detected by examining external structures (COE, 1944). However, the development of a technique allowing direct sampling of the gonadal contents of suspected protandric species that lack external characters (*e.g.*, patellacean limpets) (WRIGHT & LINDBERG, 1979) enabled us to monitor directly protandry in the limpet *Lottia gigantea* (Sowerby, 1834) (WRIGHT & LINDBERG, 1982).

In this paper we report results of initial experiments to determine the ecological and interactive factors influencing sex change in *L. gigantea*. Although our results are not entirely conclusive, we present them because these data suggest a complicated pattern of sex change involving ecological factors, lag periods, and possibly genetic probabilities of sex change within the population. It is our intention to bring these data to the attention of other workers so that possible antagonistic or synergistic effects of these phenomena are not confused or overlooked in other studies.

MATERIALS AND METHODS

Lottia gigantea is a large, territorial, intertidal limpet, sometimes reaching lengths over 100 mm (STIMSON, 1970). Larger individuals occupy either isolated territories (usually surrounded by sessile invertebrates such as barnacles and mussels) (Figure 1) or contiguous territories (where they occur at such high density that territorial boundaries are impossible to discern) (Figure 2). Younger, smaller



Explanation of Figures 1 and 2

Figure 1. Low density experimental treatment on San Nicolas Island, California.

Figure 2. High density experimental treatment on San Nicolas Island, California.

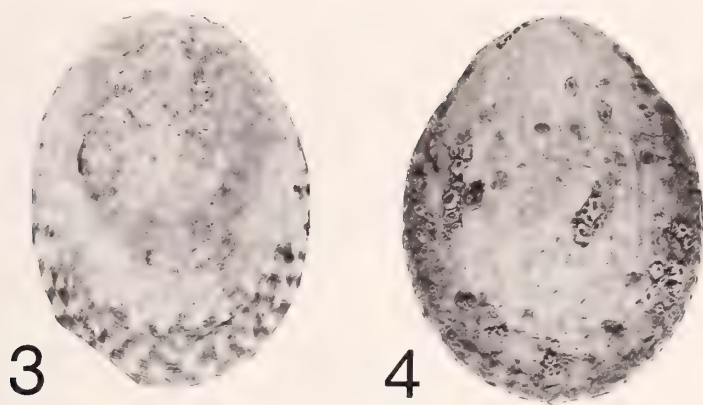
individuals typically graze on the territories of larger individuals and respond to contact with the resident limpet by escaping to the perimeter of the territory before the resident can respond aggressively (WRIGHT, 1982). Most limpets can be categorized behaviorally as either intruders or residents; intruders are always evasive while residents are usually aggressors (WRIGHT, 1982).

The growth of *Lottia gigantea* is relatively indeterminate; although each habitat imposes a maximum size above which no limpet can grow, that size ranges from 40 mm to above 70 mm depending on characteristics of the habitat (*i.e.*, density of other grazing herbivores, intertidal height, wave exposure, substratum, *etc.*). In addition, individual growth varies inversely with size relative to the local maximum (Wright, unpublished data). Thus, a 40-mm limpet in a local population where the maximum size is near 40 mm is growing slowly, if at all, and generally will be older than a 40-mm limpet in a population where the maximum size is nearer to 70 mm. We quickly realized that older, slower growing limpets could be recognized by their heavily eroded shells (Figure 4) while younger, fast growing limpets could be recognized by the checkerboard pattern of

their shells (Figure 3). Using these criteria, we could roughly judge the relative age of *L. gigantea* by external appearance within a habitat.

Experimental manipulations of *Lottia gigantea* were done on San Nicolas Island, Ventura County, California (33°16'N, 119°30'W) between December 1980 and December 1982. In all treatments, the experimental limpets were removed from the substratum while moving (to avoid trauma) and sexed by sampling the gonad through the rear body wall with a hypodermic syringe (WRIGHT & LINDBERG, 1979). The dorsal surface of the shell was marked with a plastic number embedded in waterproof epoxy before the limpet was placed in either a low (Figure 1) or high density (Figure 2) setting.

The first experiment, begun in December 1980, tested the hypothesis that high density lowers the probability of sex change. The experiment was performed with 35 males, all of which were observed to exhibit evasive behavior. Of these 35, 26 were placed on isolated empty territories (low density) where food supply was abundant and detrimental interactions with other *Lottia gigantea* nil. Seven males were placed in a high density setting of limpets with in-



Explanation of Figures 3 and 4

Figure 3. *Lottia gigantea*. Young, checkerboard specimen; length = 55 mm.
Figure 4. *Lottia gigantea*. Old, eroded specimen; length = 60 mm.

discernable boundaries. In such settings, food would be sparse and interactions frequent and potentially detrimental.

The second experiment, begun in December 1981, was designed to test the effect of age on the probability of sex change. We selected 35-mm to 45-mm 'old' and 'young' males by using the shell erosion criterion discussed above. We placed all of these in a high density treatment identical to the high density treatment in the first experiment.

At the end of each year (December) the gonadal contents of the limpets were sampled. Limpets that had become female were removed from the experimental settings and dissected to verify sex change and to check for possible

simultaneous hermaphroditism. Males were replaced in their experimental positions.

RESULTS

The results of the high and low density experiments are shown in Figure 5 and Table 1. Also included in the figure are data for *Lottia gigantea* sex change from WRIGHT & LINDBERG (1982).

The proportion of males changing sex during the first year was low in all treatments (0.08 to 0.15) and did not appear to be affected by density or age (χ^2 , $P > 0.05$). During the second year, 9 out of 11 in the low density treatment changed sex versus only 1 out of 5 in the high density treatment. These were not significantly different proportions (Fisher's exact test, $P = 0.071$) perhaps due to the low numbers in the high density treatment. In fact, the only significant difference throughout all treatments was between the limpets in the low density treatment at

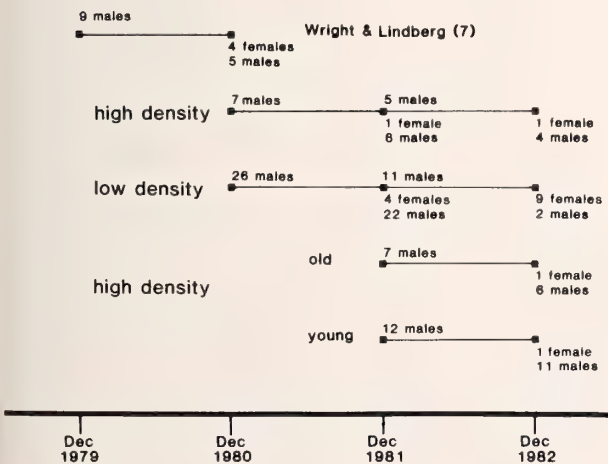


Figure 5

Patterns of sex change in *Lottia gigantea*. Number of males monitored during the experiment appears above the line, results below the line. ■ = monitoring times, (7) = (1982).

Table 1

Percent and number of male *Lottia gigantea* changing sex in various treatments. Lines connecting treatment percentages indicate significant differences at the 0.05 level or greater (Fisher's exact test). All other proportions not significantly different ($P \geq 0.05$).

Treatment	Percent changing sex and (n's)	
	First year	Second year
High density (HD)	14% (1/7)	20% (1/5)
HD Old	14% (1/7)	—
HD Young	8% (1/12)	—
Low density	15% (4/26)	82% (9/11)

the end of two years, and any of treatments at the end of one year.

No simultaneous hermaphrodites were found.

DISCUSSION

Formally, our data support nothing more than the statement that "limpets in the second year of a sex change experiment change sex more than during the first year." There are two interpretations of this conclusion. (1) The limpets that were used in the density experiment (both treatments) were all of similar age and sex change is age-specific. (2) Limpets respond to changes in environmental conditions (*i.e.*, abundant food, no agonistic losses) by changing sex, but there is a lag period greater than 12 months but less than 24 months between environmental change and sex change. We favor the second interpretation for several reasons. First, based on a preliminary aging technique, there does not seem to be any single age for sex change (Wright, personal observation). Males can be found that are probably 5 years or older, and females can be found that are probably no more than 1½ years old. Secondly, the results of the high density, young versus old experiment (Figure 5, Table 1) argue against the presence of an age-specific sex change phenomenon. Finally, the proportion of sex changers during the second year in low (9/11) versus high (1/5) density treatments, although not statistically significant, is highly disproportional—a fact that cannot stand alone given statistical convention, but that can tip the scales of a close argument. Thus, we favor the second hypothesis and the presence of environmental sex determination in *Lottia gigantea*.

In addition to the evidence supporting environmental sex determination in *Lottia gigantea*, there is a second intriguing pattern present in the data. This is the proclivity of about 15% of the population to change sex annually regardless of environmental setting or age (Table 1). This pattern may represent a genetically programmed sex change component that is virtually immune to environmental factors. Thus, sex change in *L. gigantea* may be regulated by two mechanisms: (1) environmental sex determination and (2) genetically programmed sex change. Another explanation for the persistent low proportion of sex changers in our treatments is that the limpets that changed had experienced an environmental release the year before they were used in the experiment. A final possibility is that the sex changers were simply responding to variations within the two treatments. Although we cannot rule out any of these possibilities, it is unlikely that all of the treatments we set up in December of 1980 and again a year later in December of 1981 all received similar proportions of these predisposed changers and/or had similar environmental variabilities within the study sites.

Neither environmental nor genetically programmed sex determination was suggested by the results of our first experiment (WRIGHT & LINDBERG, 1982; Figure 5 herein). We believe that the high proportion of sex chang-

ers in our first experiment (4/9) resulted because we confounded limpets with different histories. Although we carefully chose limpets that were about the same size, we did not know the territorial status of the limpets, and therefore, our experiment undoubtedly contained both intruders and residents. Thus, some of the males that changed sex may have been in low density situations for as much as a year prior to our using them in the experiment, and our results therefore include both environmentally determined sex changers that were programmed to change sex the year before, as well as limpets that were genetically programmed to change sex that year. Because of this complication, we do not feel that the earlier data set can be combined or compared with the data set presented herein.

In most previously studied protandrous marine invertebrates (see review by HOAGLAND [1978]) sex change is predominately genetically regulated or environmentally determined. In the echiuroid genus *Bonellia* both environmental sex determination and genetic sex determination appear to be important (GOULD-SOMERO, 1975; LEUTERT, 1975). In *Bonellia* the two different mechanisms of sex change are thought to represent two different genotypes in the population. The first contains "true" males and females that are genetically determined and do not change sex; the second contains a genotype in which sex is environmentally determined.

Scenarios to explain protandry in patellacean limpets have relied exclusively on genetic interpretations, including rather elaborate hypotheses with two or more genotypes in the population, representing true males and females and individuals changing sex at different ages (MONTALENTI & BACCI, 1951). Recent analysis of static sample data for *Patella vulgata* in England has identified an age-specific property associated with sex change (BAL-LANTINE, 1961; CHARNOV, 1982) and BRANCH (1974a) has presented data for *Patella oculus* (Born, 1778) from South Africa that strongly suggest an age-specific genetic mechanism. However, for *Lottia gigantea* and many other species of patellacean limpets age- and/or size-specific sex change and its resulting sex ratios are less apparent in static samples. Typically there are both small females and large males present in these samples. Moreover, the switch in the sex ratio from predominately males to predominately females is not sharp, but spread over several age or size classes (BRANCH, 1974b; WRIGHT & LINDBERG, 1982).

The tendency for workers to propose multiple genotypes for some protandrous species may result from an observation bias. In studies of species in which sex change can be externally observed (*e.g.*, in the Calyptraeidae) sex change is often found to be a response to environmental change. However, there has been no such conclusion for molluscan species in which gender can be determined only once. Instead, genetic control alone is postulated to be responsible for sex change. Workers on this latter group of species have had to complicate their genetic hypotheses in order to explain the apparently large variation in the

timing of sex change; such variation is inferred from the wide distribution of sexes as a function of size. Thus, they must further hypothesize the existence of one or more additional genotypes that change sex at different ages and/or a genotype that does not change sex at all. Missing from these discussions is the possibility of environmental sex determination, in spite of its utility in explaining highly variable size of sex change (*i.e.*, a highly variable or complex environment). Based on the results presented here, we can rule out to some extent the importance of the different-genotype hypothesis because under no conditions would it predict that such a high proportion of limpets as 9 out of 11 would change sex.

We have presented data suggesting that environment (including the social interactions among conspecifics) can control to some degree when sex change occurs in *Lottia gigantea*. We believe that our experiments suggest environmental control as an alternative hypothesis to multiple genotypes in explaining the causes of sex change in other patellacean limpets, especially when the limpet shows territoriality and/or other indications of profound environmental and/or social changes during its ontogeny (BRANCH, 1974b, 1975).

The ultimate cause of sex change in patellacean limpets is hormonal (CHOQUET, 1969). We have attempted to identify and elucidate proximate causes that can result in the patterns of sex change seen in our experimental manipulations and in static population samples. Although preliminary, we present them because they indicate that mechanisms could be overlooked if experimental manipulations are not followed for at least two years or if the past histories of the manipulated animals are not known or at least limited (*i.e.*, presence of evasive behavior in *Lottia gigantea*). Moreover, our data suggest that two mechanisms (environmental sex determination and underlying genetic determination) may be present. Such multiple effects can produce results that are difficult to interpret in static samples, short term experiments, or in traditional paradigms, and may ultimately lead to an incorrect interpretation of the mechanisms or an understatement of the processes controlling sex change.

ACKNOWLEDGMENTS

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Sediment Correlates to Density of *Crepidula fornicata* Linnaeus in the Pataguanset River, Connecticut

by

STEPHEN H. LOOMIS AND WENDY VANNIEUWENHUYZE

Department of Zoology, Connecticut College, New London, Connecticut 06320

Abstract. Relationships among the density of *Crepidula fornicata* and various characteristics of the sediments with which it is associated in the Pataguanset River, Connecticut, were examined. The population is located in an area transitional between a relatively deep channel and an intertidal sand flat. Over 90% of the stacks were situated so that most of the snails were in direct contact with a soft, silty substrate. The density of snails ranged from 0 to 43 individuals/m² and the greater densities were associated with sediments that had a high percent cover of solid substrate, relatively high silt and clay content, small mean grain diameter, and high organic content. Multiple regression analysis indicates that 67% of the variance in density can be attributed to changes in percent cover of solid substrate and another 19% of the variance in density can be attributed to changes in the organic content. The rest of the independent variables did not significantly correlate with variance in density. The significance of these data in relation to the ecology of *C. fornicata* is discussed.

INTRODUCTION

THE RELATIONSHIP between benthic organisms and various characteristics of the substrates with which they are associated has been of interest to ecologists for a long time (BADER, 1954; THORSON, 1966; SANDERS, 1958, 1960; DRISCOLL & BRANDON, 1973; DRISCOLL, 1967; RHOADS & YOUNG, 1970; CRAIG & JONES, 1966). A basic generalization that has emerged from studies on fauna-sediment relationships is that epifaunal suspension feeders are usually associated with coarser-grained or firm bottoms while deposit feeders are usually associated with finer-grained or soft substrates (DRISCOLL & BRANDON, 1973; DRISCOLL, 1967; RHOADS & YOUNG, 1970; SANDERS, 1958, 1960; CRAIG & JONES, 1966). One apparent exception to this generalization is the association of the epifaunal suspension feeder, the slipper shell *Crepidula fornicata* Linnaeus, 1758, with soft muddy substrates (DRISCOLL, 1967; DRISCOLL & BRANDON, 1973; BARNES *et al.*, 1973).

It has been suggested that this apparent anomaly can be explained by the fact that individuals of *Crepidula fornicata* are found in stacks, raising them far enough above the soft bottom to prevent fouling of their feeding mechanisms by suspended or resuspended sediment (FRETTER & GRAHAM, 1962; DRISCOLL, 1967). However, using scuba, we have observed living populations of this organism in which most of the stacks were lying on their sides buried at least one centimeter in the soft, silt substrate. Be-

cause they can live in direct contact with silt substrates, there may be other explanations for this anomaly. This paper examines changes in the density of a *C. fornicata* population in the Pataguanset River, Black Point, Connecticut (Figure 1) along a gradient of sediment types ranging from coarse sand and pebbles at the mouth of the river to soft mud 230 m upstream, in an attempt to elucidate effects of substrate type on the biology of these animals.

MATERIALS AND METHODS

Density of the animals was measured using scuba along 50-m transects by counting all of the animals in consecutive 1-m² quadrats. At the same time, the number of snails in each stack and the objects to which the snail at the bottom of each stack was attached were recorded. Bottom water samples were collected using a LaMotte water sampling bottle. The salinity of the water samples was measured with an American Optical, temperature-compensated refractometer and the temperature of the samples was measured using a mercury thermometer. Bottom topography was mapped using a surveyor's level and leveling rod.

A total of 21 transects was examined for the presence of *Crepidula fornicata*. Transect 1 was located on the east side of the mouth of the Pataguanset River and consecutive transects were 20 m apart. Each transect was situated

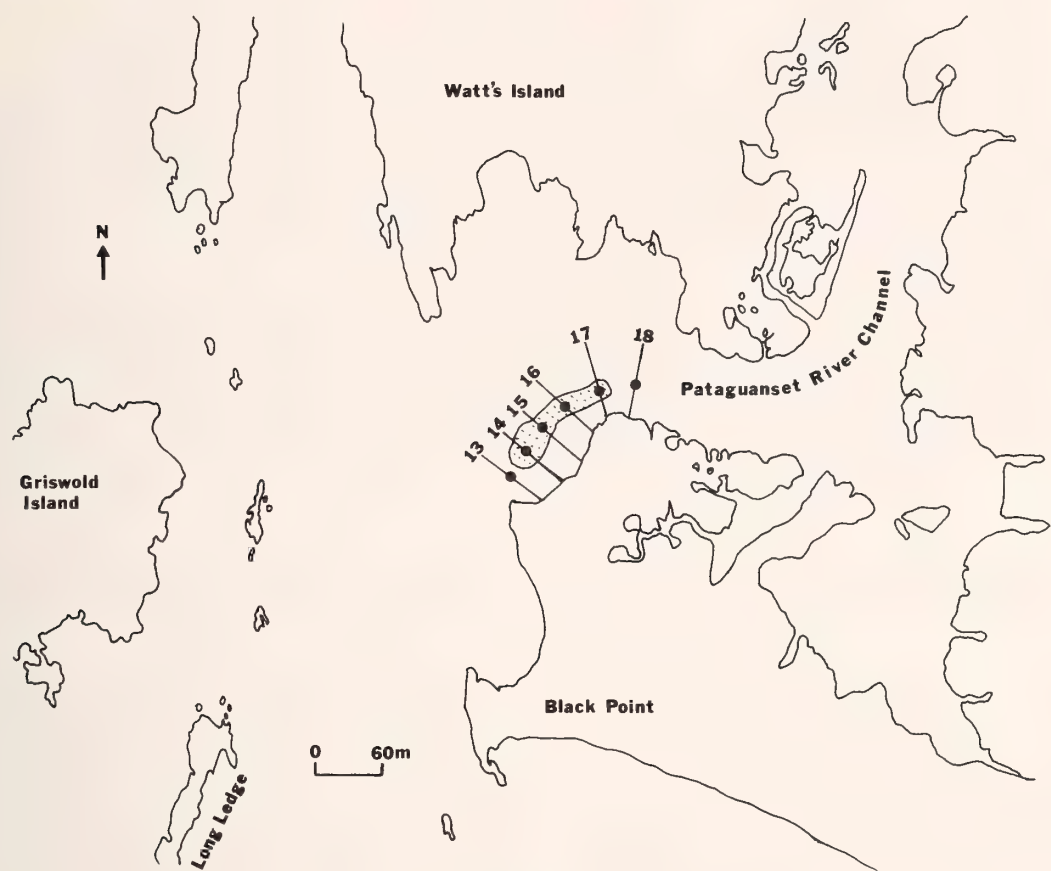


Figure 1

Map of the study area showing the location of transects 13 through 18, the limits of the population of *Crepidula fornicata* (the stippled area), and the location of the sample stations (black dots).

perpendicularly to the shoreline. This examination showed that there was a population of *C. fornicata* associated with transects 14 through 17 (Figure 1). The rest of the transects were either void of *C. fornicata* or contained only one or two stacks. The density of the snails was highest on transect 16 and fell off rapidly either upstream or downstream (Table 1). The highest density for each transect was always found approximately in the center of the population. The quadrat on each transect with the highest density was chosen as a sediment sampling station (Figure 1). Two other stations with no snails were identified on transects 13 and 18 by extrapolating the location of the population to these transects. These stations, therefore, represented areas that had densities ranging from 0 to 43 snails/m². Four sediment samples (approximately 200 g each) were collected at each station by scooping the top 2 cm of the sediment into a wide-mouth jar and immediately capping it. The samples were washed in distilled water to remove salt, centrifuged at 12,000 × *g* for 30 min, and oven dried at 75°C. Two of the samples were separated

according to particle size using a series of U.S.A. Standard Testing Sieves and each size class was weighed to the nearest 0.1 g. The silt and clay fraction (particles less than 4.20 ϕ [0.055 mm]) for each sample was suspended in 50 mL of distilled water in a graduated cylinder and particles were separated according to size classes by the pipetting

Table 1

Location of the sediment sampling stations and density of *Crepidula fornicata* at each station.

Transect	Quadrat no.	Density (snails/m ²)
13	25	0
14	33	17
15	42	36
16	38	43
17	17	27
18	19	0

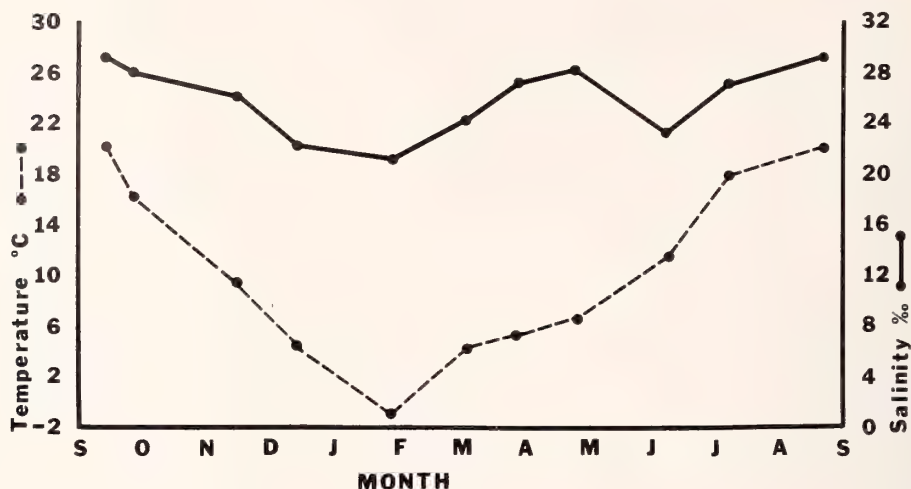


Figure 2

Temperature and salinity of water taken from the station on transect 15 from September 1981 to August 1982.

method of KRUMBEIN & PETTIJOHN (1938). The other two samples were oven dried at 75°C, weighed to the nearest 0.1 mg, combusted at 650°C for 6 h, cooled and reweighed to obtain an estimate of the organic content of the sediment. Percent cover of solid substrate was measured by collecting all of the hard material on the surface of the sediments (including shells, rocks, bottles, and wood) in replicate 0.25-m² quadrats at each station. The outline of each piece of material was traced on graph paper, cut out, and weighed to the nearest 0.1 mg on a Mettler Balance. The weights were compared to the weight of a 4-cm² piece of graph paper to calculate the surface area covered by each piece.

Observations of the movement of particles into the mantle cavity of *Crepidula fornicata* were made in the following manner. Surface sediments collected from the study site were suspended in seawater, poured into a large glass fingerbowl, and allowed to settle on the bottom of the fingerbowl until the water was clear (usually about 3 h). Stacks of *C. fornicata* were placed on the sediments with either their left or right side down and carefully pushed into the sediments until the lower edge of the shells was about 1 cm below the surface of the sediments, corresponding to the field conditions. Observations were made immediately and at one-hour intervals for 6 h with a dissecting microscope. Initial observations indicated that postural movements of the snails were important for the movement of particles into the mantle cavity. We measured these postural movements in the following way. Stacks containing only two *C. fornicata* individuals were made by fragmenting larger stacks. The animals on the bottom of the small stacks were dissected from their shells, resulting in single individuals attached to empty *C. fornicata* shells. A small hole was drilled in the anterior-most

margin of each live snail's shell. The live snails were connected to the displacement transducer of a physiograph by tying one end of a thread to the transducer and the other end to the shell through the hole. The empty *C. fornicata* shells to which the live animals were attached were anchored in a fingerbowl (which functioned as a counterweight) by four plastic coated copper wires with one end embedded in wax. This apparatus was lowered into a battery jar containing aerated seawater and movements of the snail were recorded with the physiograph. Measurements were made in the presence and absence of sediments.

RESULTS

Physical Characteristics at the Study Site

Water temperature (Figure 2) between September 1981 and August 1982 ranged from 22°C (in August) to -1°C (in January). Bottom salinity within the population of *C. fornicata* ranged from 19 to 29‰ (Figure 2) and was never different from surface salinity. These data were taken at high tide and represent maximum values; however, the salinity at low tide was never more than 3‰ less than at high tide.

Bottom profiles (Figure 3) revealed that the *Crepidula fornicata* population was located in an area transitional between a channel 2 m deep and an intertidal sand flat. The tidal range at the study site is about 1 m and all stacks were located below this range. Tidal flow velocity at this site was high although rates were not measured. The percent silt and clay of the sediments in the study area ranged from 0.2% where there were no *C. fornicata* to 19.6% where the density was intermediate. Mean grain diameter ranged from 3.6 ϕ (0.08 mm) in areas of inter-

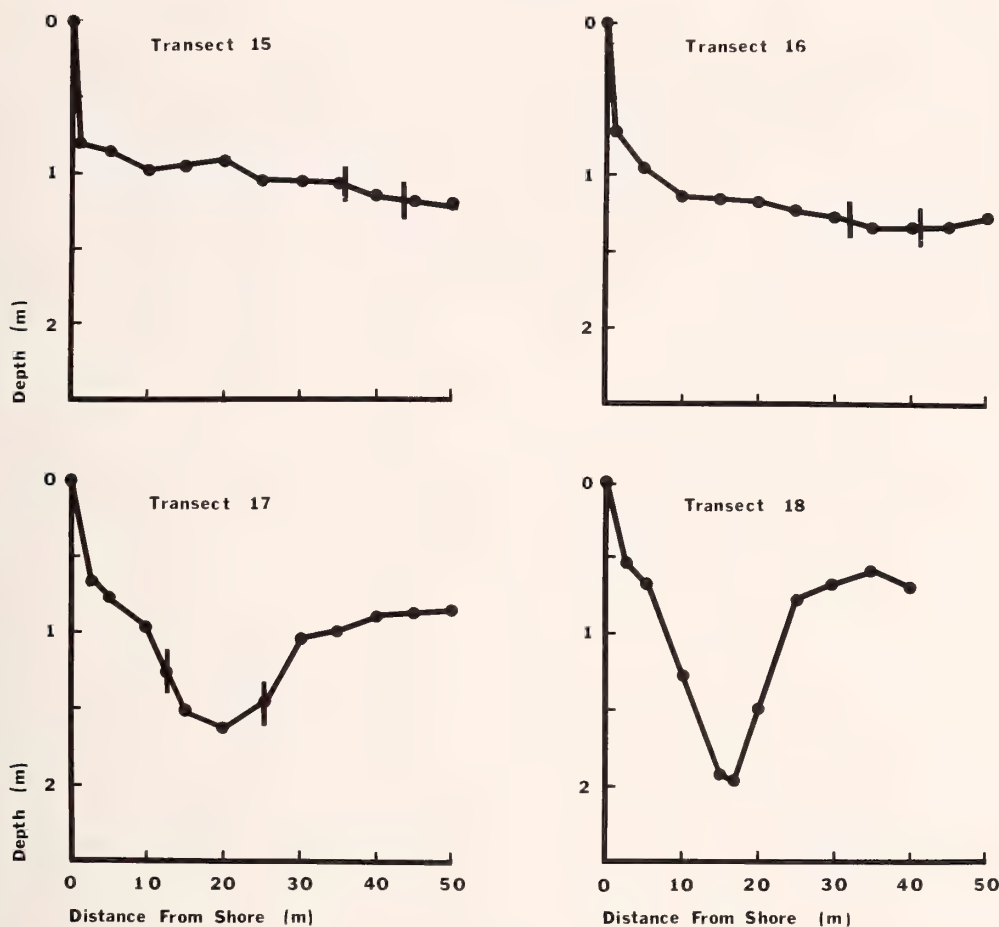


Figure 3

Bottom profile of transects 15 through 18 showing transition between channel and sand flat. Depths were taken from mean high tide. The vertical bars represent the limits of the *Crepidula fornicata* populations (there were no *C. fornicata* found in transect 18).

mediate density of *C. fornicata* to 2.4 ϕ (0.185 mm) in areas without *C. fornicata*. Sediment sorting (as measured by the Trask Sorting Coefficient) became increasingly poor with decreasing grain diameter (Figure 4). The organic content of the sediments ranged from 0.44% to 1.79%. Scattergrams of density of *C. fornicata* versus various characteristics of the sediments are shown in Figure 5. Using simple linear regression, there appears to be a positive relationship between density and the percent cover of solid substrate, ash weight, and mean grain diameter, but not with percent silt or clay (Figure 5). Simple linear regression analysis, however, does not include information on interrelationships between independent variables and, thus, may not provide an accurate assessment of relationships between the dependent variable and the combination of all independent variables. Multiple regression analysis, however, does include this information and shows that 67% of the variance in density can be attributed to changes

in the percent cover of solid material and that another 19% of the variance in density can be attributed to changes in the percent ash weight of the sediment (Table 2). The other independent variables do not significantly correlate with variance in density.

Characteristics of the Population

With the exception of a few stacks that had washed up alive on the beach, all of the specimens of *Crepidula fornicata* were located subtidally. The size of the stacks ranged from 1 to 11 animals with an average stack size of 3.8 animals. The substrates to which the live snails at the bottom of the stacks were attached, along with the percentage of total stacks attached to each kind of substrate, are shown in Table 3. Almost half of the stacks were attached to dead *C. fornicata* shells while another 34% of the stacks were attached to dead *Littorina littorea* shells.

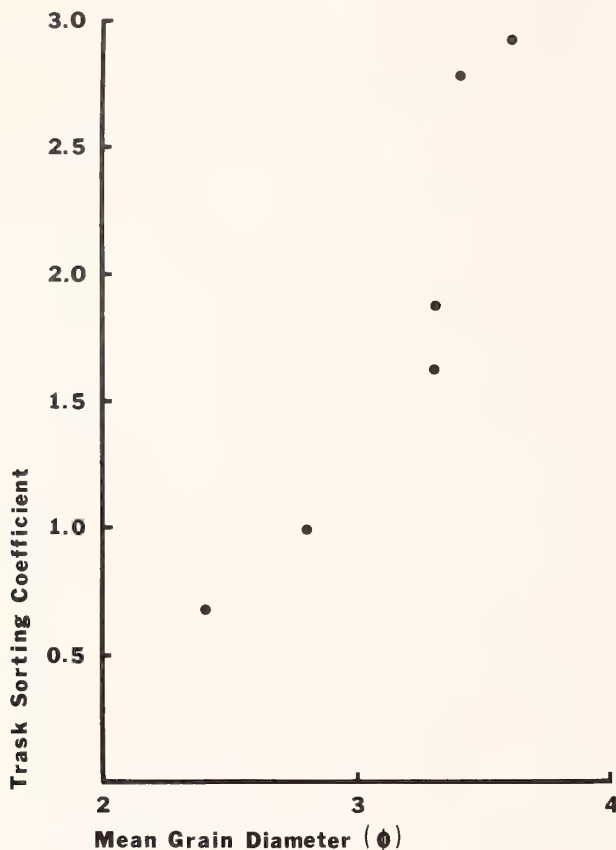


Figure 4

The relationship between mean grain diameter and the sorting of the sediments from the study site.

The rest of the stacks were attached to the shells of various dead mollusks, dead horseshoe crabs (*Limulus*), or glass bottles. All of the *C. fornicata* stacks except those attached to dead *Limulus* or bottles were lying on their right or left side and that side was buried at least 1 cm deep in the substratum with the other side exposed to water. The density of *C. fornicata* ranged from 0 to 43 individuals/m². The percent cover of solid substrate (shells, wood, and bottles), which may be a measurement of the amount of space available for the recruitment of new individuals (HOAGLAND, 1979), ranged from 0 where there were no *C. fornicata* to 9.4 where the density of snails was highest.

Behavioral Observations

Initial observations of the movement of water currents into and out of the mantle cavity of *Crepidula fornicata* indicated that postural changes of the snails might be important in feeding when the animals are associated with soft substrates. As *C. fornicata* rests upon the shell below it, an opening is produced at the anterior end where the

Table 2

Stepwise multiple regression analysis of density of *Crepidula fornicata* vs. percent cover of solid substrate (COV), organic content (OC), percent silt and clay (SC), mean grain size (MGS), and depth (DEP). NS represents no significant information added.

Variable	r^2	Change in r^2	Significance
COV	0.669	0.669	P < 0.001
OC	0.863	0.194	P < 0.05
SC	0.870	0.007	NS
DEP	0.905	0.036	NS
MGS	0.924	0.019	NS

animal's shell margin meets the lower shell. The snails appeared to undergo a cycle of movements that involved changing the width of this opening. These movements were measured using a physiograph and the results from one animal are presented in Figure 6. The cycle begins when the snail rapidly closes the aperture. This movement results in the rapid expulsion of water from the mantle cavity which resuspends sediments into the water adjacent to the animal. The aperture remains closed for a short period of time and then opens again. When the aperture is opened, water rushes into the mantle cavity. The aperture remains open while the snail filters the resuspended sediments from the water. Small movements while the aperture is open may facilitate the movement of water into and out of the mantle cavity. The cycle begins again with the rapid closure of the aperture. The postural movements have the secondary effect of clearing a free space in the sediment just below the anterior end of the animals so that water can circulate freely whether the stacks are on their right or left side. Similar results were obtained from all snails tested whether associated with sediments or not.

DISCUSSION

Crepidula fornicata in the Pataguanset River is associated with sediments that have a silt and clay content ranging

Table 3

Substrates to which *Crepidula fornicata* stacks were attached.

Substrate	Number of stacks	% of total stacks
<i>Crepidula fornicata</i>	52	44.8
<i>Littorina littorea</i>	39	33.6
Bottle	7	6.0
<i>Mytilus edulis</i>	6	5.2
<i>Mercenaria mercenaria</i>	6	5.2
<i>Limulus polyphemus</i>	5	4.3
<i>Busyon canaliculatum</i>	1	0.9

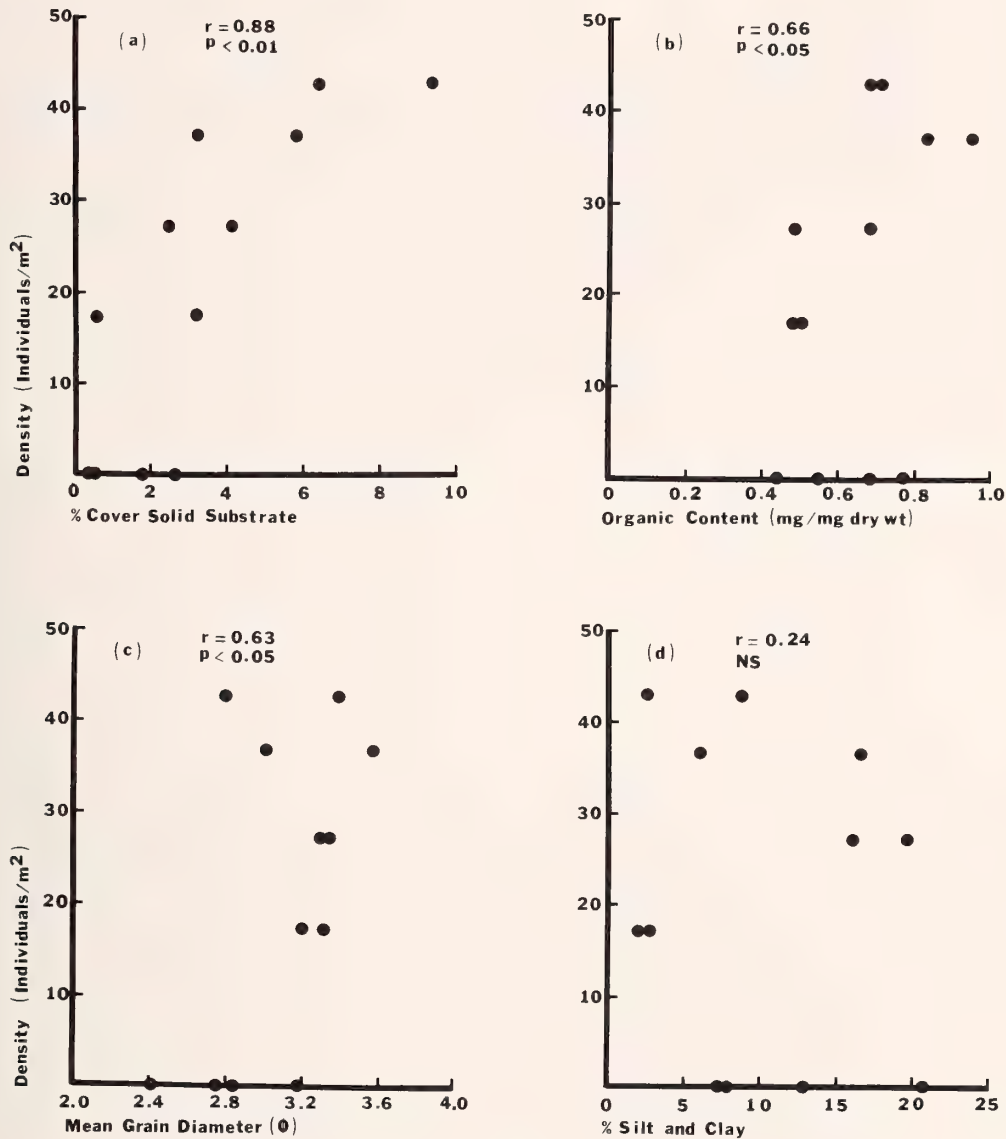


Figure 5

Scattergrams of the density of *Crepidula fornicata* vs. percent cover solid substrate (a), organic content of the sediments (b), mean grain diameter of the sediments (c), and percent silt and clay in the sediments (d) (r value and significance factors are given for linear regression of each of the independent variables).

from 0.2 to 19.6%, a mean grain diameter ranging from 3.6 ϕ (0.08 mm) to 2.4 ϕ (0.185 mm), organic content ranging from 0.44 to 1.79%, and cover of solid substrate ranging from 0.5 to 10%. The only sediment characteristics that were correlated with the density of *C. fornicata* were percent cover of solid substrate and organic content.

The correlation between cover of solid substrate and the density of *Crepidula fornicata* is not surprising considering that the larvae of the snails require a solid substrate upon which to settle (HOAGLAND, 1979). A new popula-

tion would not become established in areas that had no solid substrate, and the greater the cover of solid substrate, the greater would be the chances for the establishment of new stacks. DRISCOLL (1967) obtained similar results in a study of attached epifauna-substrate relations in Buzzards Bay, Massachusetts. He found that the highest densities of *C. fornicata* were associated with "shell-rich" substrates, although he did not present quantitative data on the amount of solid substrate present.

The correlation between the organic content of the sed-

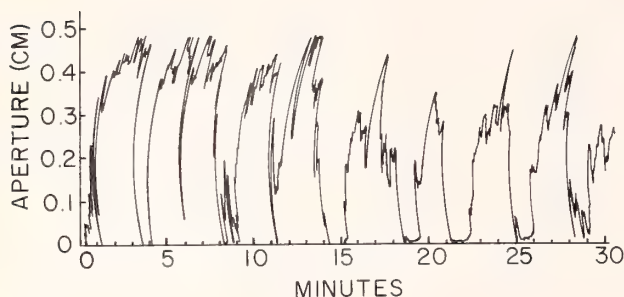


Figure 6

Physiograph recording of postural movements of an individual *Crepidula fornicata*.

iments and the density of *Crepidula fornicata* is not as easily explained. Most epifaunal suspension feeders are associated with sediments that have a low silt and clay content and a mean grain diameter in the medium sand range (SANDERS, 1958; DRISCOLL, 1967). This study and others (DRISCOLL, 1967; DRISCOLL & BRANDON, 1973; BARNES *et al.*, 1973) suggest that *C. fornicata* is anomalous in that it is an epifaunal suspension feeder but it is associated with finer grained sediments that have a high silt and clay content, high organic content, and whose sorting becomes increasingly poor with decreasing mean grain diameter. One reason that epifaunal suspension feeders are not associated with finer grained sediments may be low food availability in the water above these sediments (TURPAEVA, 1959; SANDERS, 1958; DRISCOLL, 1967). If *C. fornicata* could utilize the organic matter in the sediments as a food source, it might be able to survive on sediments that exclude other epifaunal suspension feeders. It appears that *C. fornicata* does have such a mechanism. Postural changes allow the snails to resuspend fine sediments and filter them from the water. This mechanism would require that the organic content of the sediments be high enough to satisfy the oxidative requirements of the animal. Therefore, the higher the organic content of the sediments, the more likely it is that *C. fornicata* could survive and reproduce. Another explanation for the exclusion of epifaunal suspension feeders from finer grained sediments may be that their filtering mechanism is clogged by very fine surface sediments that are resuspended by low velocity tidal flow (RHOADS & YOUNG, 1970). The efficiency of filter feeding of *Crepidula* does decrease under turbid conditions (JOHNSON, 1971), but it is likely that a

higher organic content of the sediments could compensate for this decreased efficiency.

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Histopathological and Histochemical Effects of Larval Trematodes in *Goniobasis virginica* (Gastropoda: Pleuroceridae)

by

JANE E. HUFFMAN

Department of Zoology and Physiology, Parasitology Laboratory,
Rutgers The State University, Newark, New Jersey 07102

AND

BERNARD FRIED

Department of Biology, Lafayette College, Easton, Pennsylvania 18042

Abstract. The histopathological and histochemical effects of parasitism in *Goniobasis virginica* (Gmelin, 1791) (Gastropoda: Pleuroceridae) by the rediae of *Sphaeridiotrema globulus* and *Philophthalmus megalurus* and the microphallid sporocysts of a ubiquitous type and a lecithodendriid of a virgulate type are reported. The larval stages caused extensive damage to the digestive gland and the muscle surrounding the gland either by ingesting host tissue or through increased pressure due to their sheer numbers. There was no detectable hemocyte response by the molluscan host to the presence of living rediae and sporocysts. The occurrence of dead rediae of *S. globulus* did elicit a hemocyte response. Rediae of *S. globulus* were found also in kidney and gill tissue. Decreases in glycogen, lipid, acid mucopolysaccharide, and keratin content of the digestive gland occurred in parasitized snails. Amyloid content was unchanged in parasitized snails. Double infections involving *S. globulus* and microphallid sporocysts, and *P. megalurus* and microphallid sporocysts, also occurred in *G. virginica*. Metacercariae of *S. globulus* are found free between the shell and visceral mass and do not elicit any discernable pathologic response in the snail.

INTRODUCTION

VARIOUS HISTOPATHOLOGICAL and histochemical investigations have been made on digenean larvae and their molluscan hosts (JAMES, 1965; WRIGHT, 1966; READER, 1971a, b). Previous studies have dealt with a variety of mollusks (HURST, 1927; PRATT & BARTON, 1941; CHENG, 1963a, b; PORTER *et al.*, 1967; MOORE & HALTON, 1973; BECKER, 1980) but none have involved the pleurocerid gastropod *Goniobasis virginica* (Gmelin, 1791).

Goniobasis virginica is the intermediate host for *Sphaeridiotrema globulus* in Lake Musconetcong, New Jersey (HUFFMAN & FRIED, 1983). Adults of this fluke produce ulcerative hemorrhagic enteritis in mute swans and have accounted for 142 deaths of these birds at Lake Musconetcong between September 1977 and December 1981

(ROSCOE & HUFFMAN, 1982). During the survey of *G. virginica* by HUFFMAN & FRIED (1983), four species of larval trematodes were found in this snail.

In the present investigation, a comparative study has been made on the pathological and histochemical effects of the rediae of *Sphaeridiotrema globulus* and *Philophthalmus megalurus*, the sporocysts of a microphallid of a ubiquitous type, and a lecithodendriid of a virgulate type (two different types of microphallids) on the digestive gland, muscle, kidney, and gill of *Goniobasis virginica*. Stained sections of uninfected snail tissues were compared with similarly stained sections of parasitized tissue.

The morphology and function of gastropod digestive gland cells have been disputed. SUMNER (1965) described four morphologically distinct types of cells. BARFURTH (1880), READER (1971a), and MOORE & HALTON (1973)

recognized only three, while PORTER *et al.* (1967) and PORTER (1970) reported two distinct cell types in *Oxytrema siliqua* and *Flumenicola virens* respectively. Examination of existing reports also revealed that the same cell type is designated by an assortment of names.

The studies reported here were initiated to determine (1) histologically the loci of different trematode infections within the snail host; (2) if the pathological and histochemical response varies depending upon the species of larval trematode involved; and (3) the morphology of normal digestive gland of *Goniobasis virginica* as a base for evaluating pathologic responses to larval trematode infections.

MATERIALS AND METHODS

Specimens of *Goniobasis virginica* ranging in length from 20 to 30 mm were collected from Lake Musconetcong, New Jersey, and maintained in the laboratory in a 38-L filtered aquarium containing lake water. Snails were crushed within 3 days after collection and were examined under a dissection microscope. Forty infected snails were divided into four groups of ten, with each group representing one of the four species of larval trematodes. Two groups of five snails, each doubly infected with *Sphaeriodiotrema globulus* or *Philophthalmus megalurus* and a microphallid, were processed for study along with ten uninfected snails. Parasitized and nonparasitized snails were removed from their shells and fixed in 10% neutral buffered formalin (NBF). For histopathological studies, tissues were dehydrated in an alcohol series, embedded in paraffin, sectioned at 6 μ m, and stained with hematoxylin and eosin. For the detection of neutral lipids, tissues were fixed in NBF, embedded at -20°C in an inert embedding compound used for cryostat microtomy (O.C.T.; Ames Co., Elkhart, Indiana), and sectioned at 8 μ m on a CTF microtome-cryostat (International). For histochemical studies, the tissues were dehydrated in an alcohol series, embedded in paraffin, sectioned at 6 μ m, and the following procedures (LUNA, 1968) were used: alcian blue, pH 2.5, 1.0, and 0.4 for acid mucopolysaccharides; periodic acid-Schiff (PAS) reaction for complex carbohydrates, with controls incubated in 0.5% malt diastase; Ayoub-Shklar's method for keratin (sulfur containing fibrous protein); Bennhold's method for amyloid (carbohydrate-containing protein); Oil Red O in propylene glycol for neutral lipids; Dahl's alizarin red S method for calcium salts; Oil Red O method for lipofuchsin; and Gomori's one step trichrome for connective tissue.

RESULTS

Morphology

The uninfected digestive gland of *Goniobasis virginica* is orange or brown and occupies the upper whorls of the shell. The digestive gland consists of numerous tubules surrounded by loose connective tissue containing the vis-

ceral hemocoelic space. The tubules are separated from the hemocoel by a thin layer of loose connective tissue and lined with glandular epithelium (Figure 1). This epithelium is composed of two cell types, serous and mucous cells. The serous cells are triangular. The cytoplasm at the base of each cell is basophilic. The nucleus is round and situated close to the base of the cell. The cytoplasm toward the apex of the serous cells contains eosinophilic granules. The mucous cells are columnar with flattened nuclei which are crowded against the base of the cells. There is less basophilia at the base of these cells than in serous cells. The cytoplasm of mucous cells contains glycogen, lipid, and amyloid. The serous cells contain keratin, lipofuchsin, and calcium salts. The periphery of the digestive gland consists of muscle (Figure 2). A membrane, comprised of a single squamous epithelial layer overlying a connective tissue layer, encloses the digestive gland.

Gross Pathology Due to *Sphaeriodiotrema globulus*

The digestive glands of snails infected with the rediae of *S. globulus* are white. The rediae are readily visible as robust white organisms, each with an orange longitudinal streak. The streak is the pharynx and gut containing cellular debris of host origin.

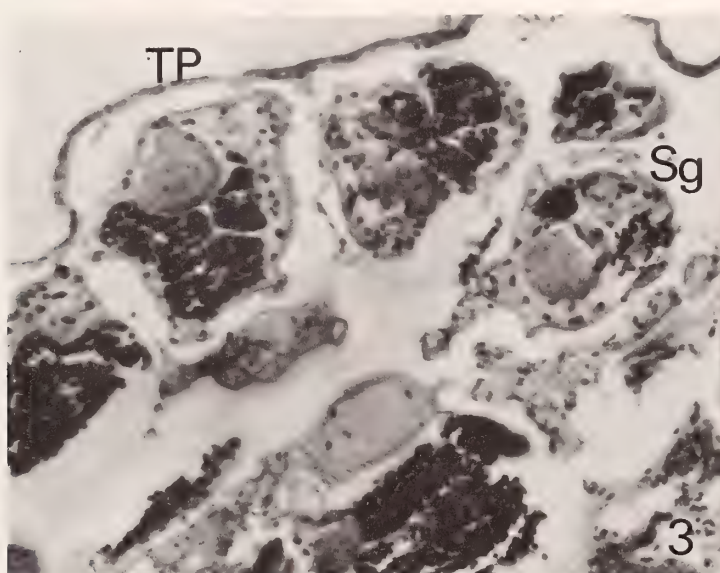
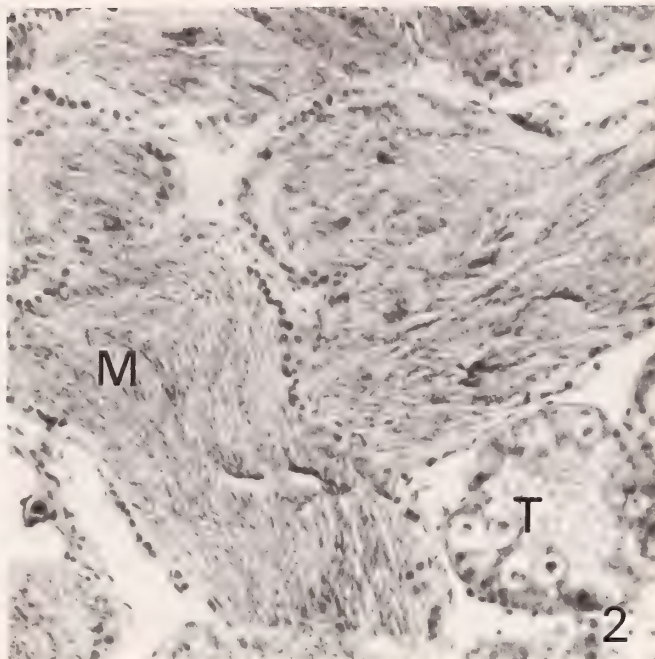
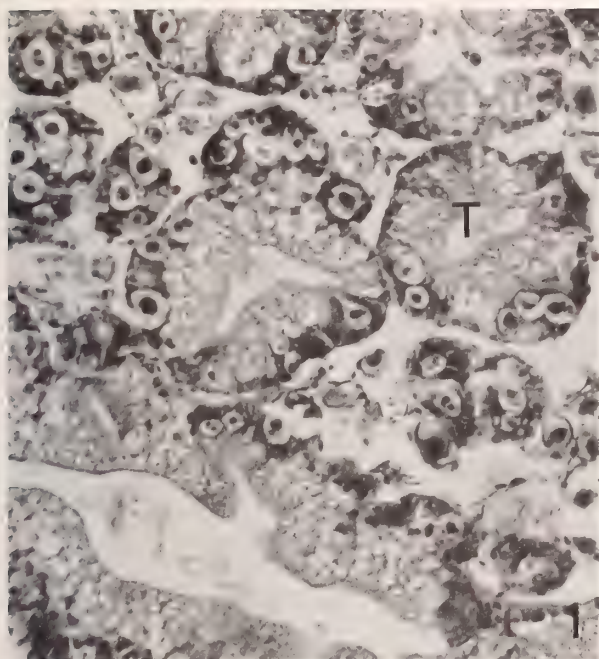
Histopathology Due to *Sphaeriodiotrema globulus*

The rediae of *S. globulus* are located mainly in the periphery of the digestive gland (Figure 3) and cause extensive damage to the muscle. Rediae are surrounded by clear zones (Figure 4) devoid of cells. There is no detectable hemocytic response on the part of the molluscan host to the presence of living rediae. In snails with dead rediae of *S. globulus*, there is a hemocytic response to the parasite (Figure 5). Dead rediae differ from live rediae in that the parasite's muscular tissue and tegument undergo autolysis with loss of cellular structure. The germinal cells within rediae appear to be more resistant to autolysis and consequently retain their normal appearance. In heavy, and also in double infections involving microphallid sporocysts, rediae are found abutting tubules in the digestive gland, in the kidney, and in gill tissue (Figures 6, 7). Digestive gland tubules in contact with rediae show reduced lumen size. The decrease in size is due to the pressure exerted by large numbers of parasites. Rediae occurring in the digestive gland disrupt the connective tissue network.

The encysted metacercariae of *Sphaeriodiotrema globulus* also occur in *Goniobasis virginica* but are free between the shell and visceral mass and do not elicit a discernable pathologic response.

Histochemistry

The digestive gland of uninfected *Goniobasis virginica* contains glycogen. Clumps of PAS-positive granules are



Explanation of Figures 1 to 3

Figure 1. Uninfected *Goniobasis virginica* digestive gland, illustrating tubule (T). H&E, 100 \times .

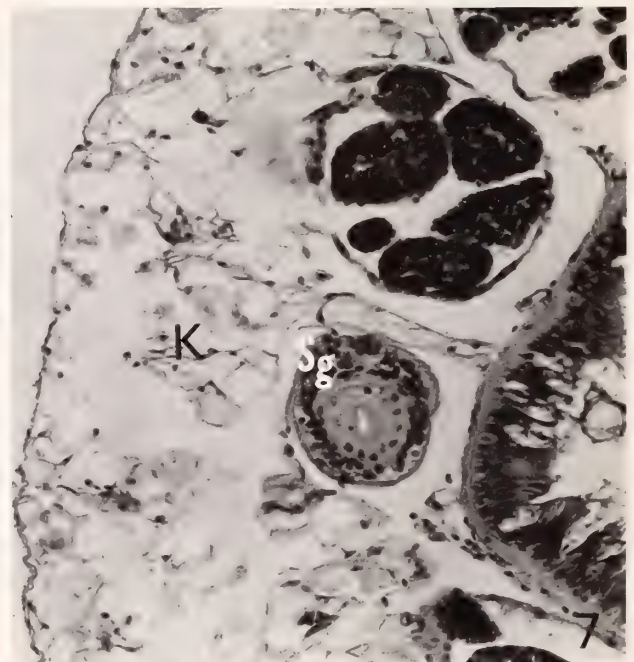
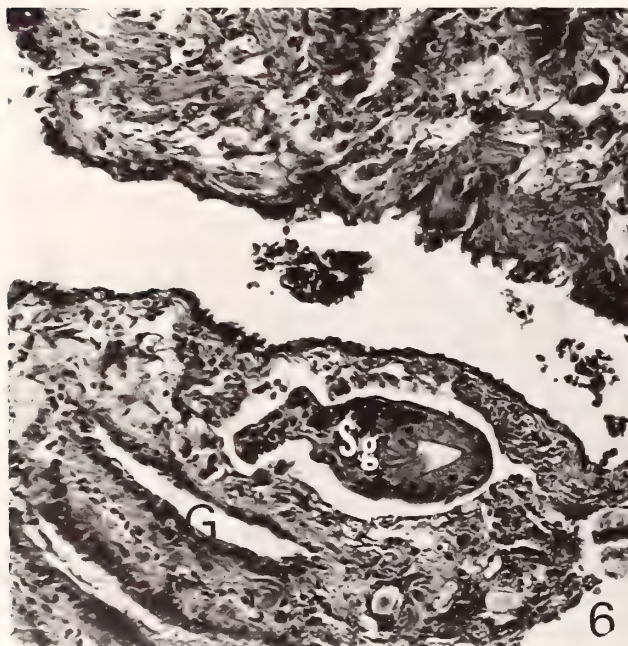
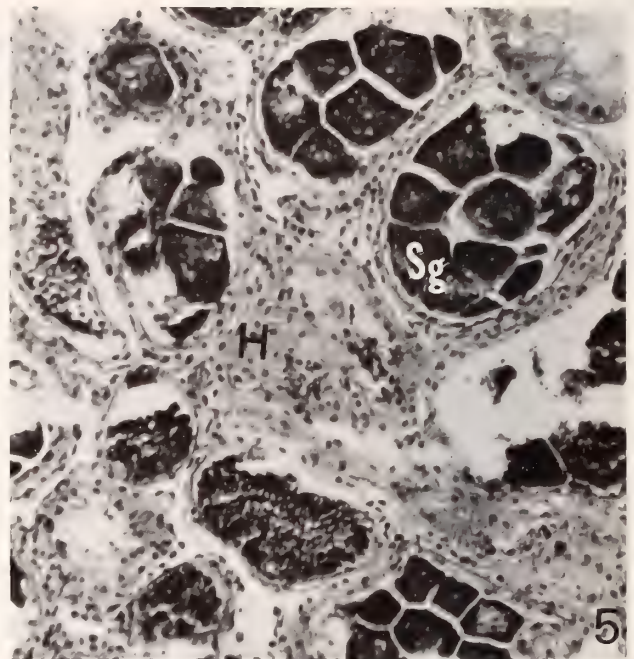
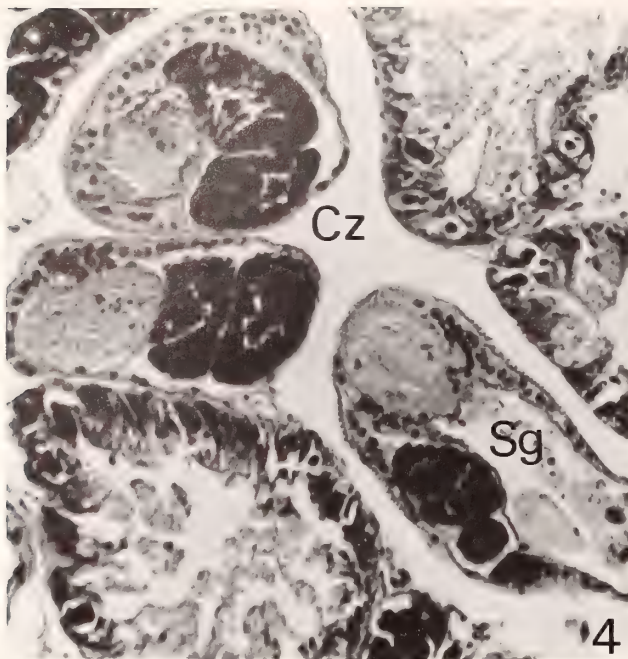
Figure 2. Uninfected *Goniobasis virginica* illustrating muscle (M) and tubule (T) of digestive gland. H&E, 100 \times .

Figure 3. *Sphaeridiotrema globulus* (Sg) rediae in the periphery of the digestive gland of *Goniobasis virginica*, also illustrating tunica propria (TP). H&E, 100 \times .

present throughout the cytoplasm of the mucous cells of the digestive gland. With the infection of the digestive gland with *Sphaeridiotrema globulus*, glycogen decreases concurrent with the presence of PAS-positive material in the rediae and cercariae of *S. globulus*.

Digestive gland cells in uninfected snails contain keratin. Keratin is present in the rediae and cercariae of *S. globulus* but host stores are not depleted. Dead *S. globulus* rediae are surrounded by a thin layer of keratin.

Acid mucopolysaccharides (pH 2.5, 1.0, 0.4) were pres-



Explanation of Figures 4 to 7

Figure 4. *Sphaeridiotrema globulus* (Sg) in the periphery of the digestive gland illustrating clear zones (Cz) surrounding the parasite. H&E, 100 \times .

Figure 5. Hemocyte response (H) to dead *Sphaeridiotrema globulus* (Sg). H&E, 450 \times .

Figure 6. *Sphaeridiotrema globulus* (Sg) redia in gill tissue (G) of *Goniobasis virginica*. H&E, 100 \times .

Figure 7. *Sphaeridiotrema globulus* (Sg) rediae in kidney (K) of *Goniobasis virginica*. H&E, 100 \times .

ent in uninfected snail digestive gland tissue and depletion occurs in snails infected with *S. globulus* rediae. Amyloid content is unchanged in parasitized snails.

In uninfected snails, neutral lipids occur in the mucous cells of the digestive gland and scattered throughout intertubular spaces. The neutral lipid content in tubules in close proximity to *S. globulus* rediae is diminished. Lipid occurs in the body wall and gut of these rediae.

Gross Pathology Due to *Philophthalmus megalurus*

The digestive gland of snails infected with the redial stages of *P. megalurus* is white and orange. The rediae are visible to the naked eye. The rediae of *P. megalurus* are more elongate and not as robust as those of *Sphaeridiotrema globulus*.

Histopathology Due to *Philophthalmus megalurus*

The rediae of *P. megalurus* are located in the periphery of the digestive gland and cause extensive disruption of the myofibers in the periphery of the gland (Figure 8). This parasite also invades the digestive gland (Figure 9), causing decreased tubular lumen size due to the pressure exerted by the parasite and disrupting the connective tissue network. There is no host hemocytic response to the living rediae. Rediae are surrounded by clear zones devoid of cells.

Histochemistry

Glycogen and neutral lipid depletion occur in snails infected with *Philophthalmus megalurus*. Glycogen is present within the redial gut and body wall. Only tubules in close proximity to parasites revealed a decrease in neutral lipid content. Neutral lipid occurs in the body wall and gut of the rediae.

Keratin occurs within the rediae and cercariae of *P. megalurus*. The host digestive gland cells and muscles are devoid of the substance. Rediae and cercariae accumulate acid mucopolysaccharides concurrent with depletion from host tissue. Amyloid content is unchanged in parasitized snails.

Gross Pathology Due to Ubiquita Microphallid and Virgulate Lecithodendriid

The daughter sporocysts of the microphallid and the lecithodendriid are not visible to the naked eye; therefore, gross pathology is not discernable. Once the snail tissue is dissected, the small white rounded structures can be seen with a dissecting microscope.

Histopathology Due to Ubiquita Microphallid and Virgulate Lecithodendriid

The microphallid and lecithodendriid sporocysts are located primarily in the visceral hemocoelic spaces of the digestive gland (Figure 10). Digestive gland tubules in

contact with sporocysts show a reduced lumen. There is disruption of the connective tissue network. In heavily infected snails, the digestive gland is reduced substantially from its normal size. Sporocysts become intimately associated with the digestive gland tissue and some sporocysts abut the digestive tubules (Figure 12). The thin connective sheath surrounding the tubule remains intact.

Histochemistry

Depletion of acid mucopolysaccharides (pH 2.5, 1.0, 0.4) occurs with both of the sporocyst infections. Abundant amounts were found within the sporocysts. Glycogen and neutral lipid depletion also occurred in both sporocyst infections. Glycogen granules were associated with the sporocyst body wall. Neutral lipids were demonstrated in developing cercariae. Amyloid content was unchanged; trace amounts do appear in the sporocysts.

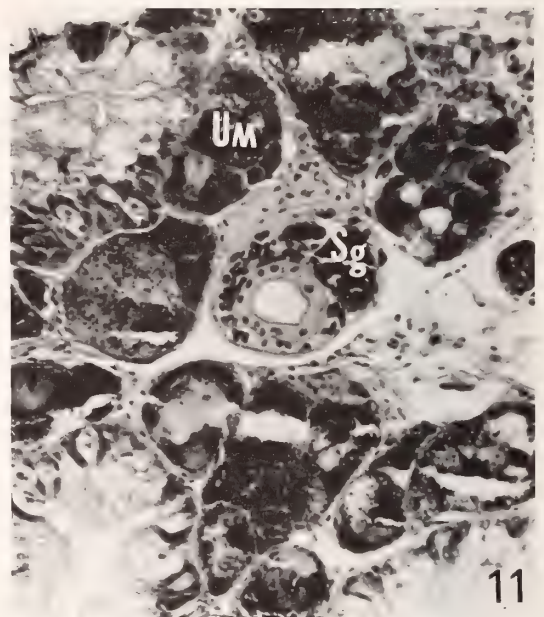
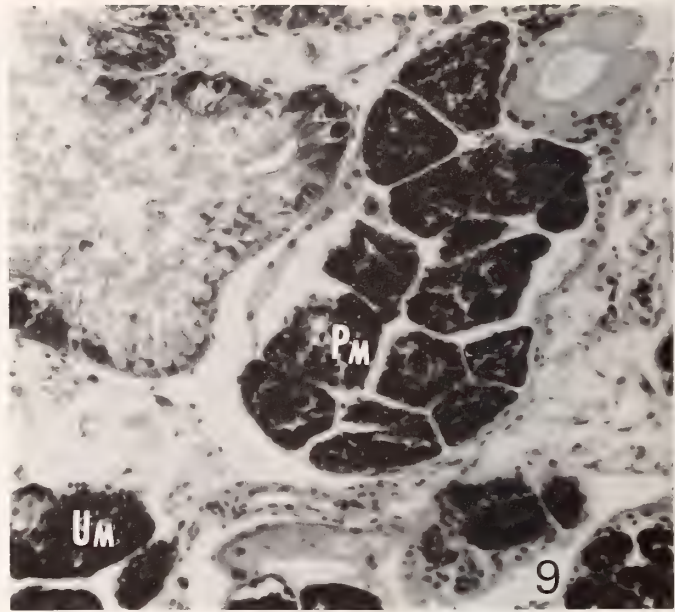
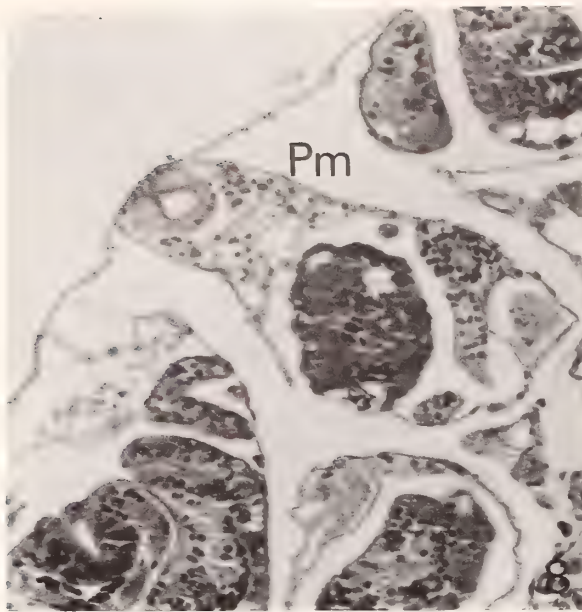
In double infections (Figure 11), the observations were the same as for single infections involving *Sphaeridiotrema globulus*, *Philophthalmus megalurus*, and the microphallid. The double infections occupy the periphery of the digestive gland, kidney, and gills of infected snails.

DISCUSSION

Despite numerous studies of the gastropod digestive gland, there is little agreement on the terminology and classification of cell types. PAN (1958) described three cell types in the digestive gland of *Biomphalaria glabrata*: goblet, lime, and digestive. SUMNER (1965) described four types of epithelial cells in *Helix aspersa*. PORTER *et al.* (1967) recognized two types in *Oxytrema siliqua*: liver and calcium cells. READER (1971a) recognized three types in *Bithynia tentaculata*: absorptive, secretory, and thin cells. MOORE & HALTON (1973) described three cell types in *Lymnaea truncatula*: digestive, mucous, and basophil cells.

Absorptive cells have previously been called liver, ferment, digestive, secretory, or excretory cells. Secretory cells have previously been referred to as lime, calcium, or excretory cells. Mucous and serous secreting cell types are present in *Goniobasis virginica*. The epithelial cells of the digestive gland in this gastropod have morphological characteristics typical of mucous and serous secreting columnar epithelium. These two morphologically distinct types are further differentiated on the basis of their cytoplasmic constituents identified by histochemical analysis.

Numerous studies have been made on the destruction of molluscan digestive gland by larval trematodes (FAUST, 1920; AGERSBORG, 1924; HURST, 1927; PRATT & BARTON, 1941; CHENG & JAMES, 1960; CHENG & SYNDER, 1962a, b, 1963; PORTER *et al.*, 1967; READER, 1971b; MEULEMAN, 1972; YOSHINO, 1976; TRIPP & TURNER, 1978). In the present study, the rediae of *Sphaeridiotrema globulus* and *Philophthalmus megalurus*, sporocysts of a microphallid and a lecithodendriid trematode have some pathological effects on the tissues of *Goniobasis virginica*.



Explanation of Figures 8 to 11

Figure 8. *Philophthalmus megalurus* (Pm) infection in *Goniobasis virginica*. H&E, 100 \times .

Figure 9. *Philophthalmus megalurus* (Pm) redia and sporocyst of a ubiquita microphallid (Um). H&E, 450 \times .

Figure 10. Sporocysts of a ubiquita microphallid (Um) in the digestive gland (tubule, T) of *Goniobasis virginica*. H&E, 450 \times .

Figure 11. Double infection of the digestive gland with *Sphaeridiotrema globulus* (Sg) and a ubiquita microphallid (Um). H&E, 100 \times .

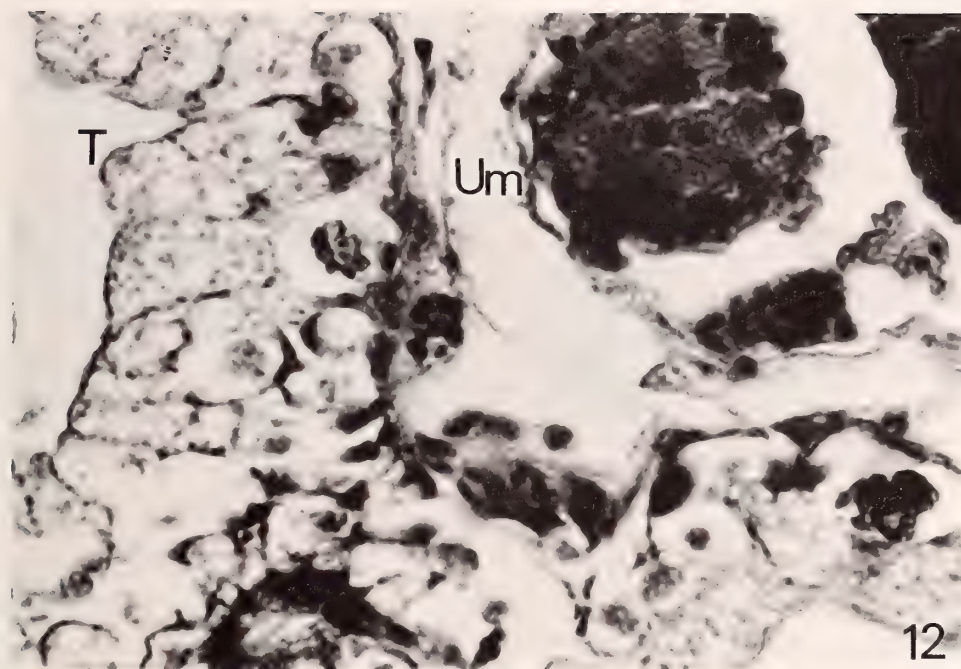


Figure 12

Sporocyst of a ubiquitous microphallid (UM) abutted to a tubule (T) in the digestive gland of *Goniobasis virginica*. H&E, 1000 \times .

One difficulty in studies employing naturally infected snails is that the sequence of pathology cannot be determined nor the long term consequences of infection on the initial changes that occur at the beginning of infection.

The primary method of cell destruction and removal by rediae of *Sphaeridiotrema globulus* in the digestive gland appeared to be through ingestion. This was indicated by the presence of host cellular debris in the redial gut. CHENG (1963c) observed similar changes in *Helisoma trivolvis* infected with *Echinoparyphium* sp. rediae. The rediae and sporocysts reported in our study no doubt exerted mechanical pressure on the digestive gland tubules as evidenced by constricted tubular lumens. It is also possible that the excretory products of the rediae and sporocysts had a lytic effect on host tissue, as evidenced by the clear zone around living trematodes. The clear zones were devoid of cells and these zones may be edematous.

A hemocyte response to dead *Sphaeridiotrema globulus* rediae was noted but no reaction occurred in response to living larval trematodes. Many workers have noted little or no cellular response to living trematode larvae in their molluscan hosts (CHENG, 1963b; CHENG & BURTON, 1965; JAMES, 1965; FENG, 1967; LOKER, 1978). Mechanisms by which living parasites inhibit the ability of the mollusk to recognize them as foreign is unknown (FONT, 1980). Dead trematodes lose this capability and are attractive to the hemocytes of the snail. MEULEMAN (1972) noted infiltra-

tion of hemocytes to foci of cellular necrosis as the result of trematode activity.

Impairment of the digestive gland function may occur as the result of *Goniobasis virginica* heavily infected with larval trematodes. Whether or not this impairment has an effect on survival of the snail is not known. CHENG & SYNDER (1962a) reported that *Helisoma trivolvis* heavily infected with *Glythelmins pennsylvaniensis* can survive the infection.

Many of the effects of intramolluscan parasites on the host's metabolism are known but difficult to generalize (BECKER, 1980). The digestive gland of uninfected *Goniobasis virginica* contains glycogen which appears as granular material scattered throughout the cytoplasm. In snails infected with either sporocysts or rediae there was a decrease in the glycogen content of the digestive gland cells. Concurrent with the depletion of host glycogen was an increase in the glycogen content of developing parasites. This depletion suggests the utilization of host glycogen by these larval digeneans. The rediae probably derive most of their glycogen by ingesting host cells. They may also absorb nutrients through their body walls, but glycogen is most likely too large to pass through the digenean body wall (CHENG & SYNDER, 1963). Glycogen from the host digestive gland is most likely hydrolyzed to monosaccharides which pass out of gland cells into intertubular spaces. A decrease in neutral lipid content was also evident in

snails infected with either sporocysts or rediae. This also suggests utilization of host lipid by these larval parasites. The effects of glycogen and lipid depletion have been extensively studied in various molluscan hosts by CHENG (1962, 1963a, b, c, 1965), CHENG & SYNDER (1962a, b, 1963), CHENG & BURTON (1966), JAMES (1965), PORTER *et al.* (1967), NEGRUS (1968), READER (1971a), and ROBSON & WILLIAMS (1971).

Keratin, a fibrous protein, was found to be substantially depleted only in snails infected with *Philophthalmus megalurus*. This protein was reported by DIXON (1965) in the metacercarial cyst wall of *Fasciola hepatica* which encysts on vegetation. *Philophthalmus megalurus* also encysts on vegetation and the keratin uptake by this parasite may be in preparation for the encystment process. The deposition of a keratin sheath around the autolytic redia of *Sphaeriodotrema globulus* appears to be an attempt by *Goniobasis virginica* to wall off the parasite.

ACKNOWLEDGMENTS

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Architectonica (Architectonica) karsteni (Rutsch, 1934):
A Neogene and Recent Offshore Contemporary of
A. (Architectonica) nobilis Röding, 1798
(Gastropoda: Mesogastropoda)

by

THOMAS J. DEVRIES

Institute of Polar Studies, The Ohio State University, Columbus, Ohio 43210

Abstract. The subdued spiral and axial sculpture of the Miocene-early Pliocene mesogastropod *Architectonica (Architectonica) nobilis karsteni* Rutsch, 1934, has been used to distinguish it from the more granulose *A. (Architectonica) nobilis nobilis* Röding, 1798, a long-ranging and widespread species of the Caribbean and western tropical American shelf. Especially noteworthy in the former taxon is the absence ventrally of a second, noded spiral cord and a second, wide spiral groove. Discovery of Plio-Pleistocene specimens in northwestern Peru and Recent specimens from western tropical America, all referable to *A. nobilis karsteni*, suggests that this form has maintained its phenotypic, and presumably genotypic, integrity for as long as *A. nobilis nobilis*. A re-analysis of the shell morphology of *A. nobilis karsteni* and a fresh consideration of its habitat suggest that the subspecies should be accorded specific rank, namely, *Architectonica (Architectonica) karsteni* (Rutsch, 1934).

INTRODUCTION

Architectonica (Architectonica) nobilis nobilis Röding, 1798, is a low-spiral, solidly built mesogastropod characterized by its granulose texture and strong spiral sculpture. This species is a common constituent of Neogene and Recent shelf faunas of the Caribbean and eastern tropical Pacific Ocean (WOODRING, 1959; KEEN, 1971; ABBOTT, 1974). *Architectonica nobilis karsteni* Rutsch, 1934, is smoother and less sculptured than the type form. It is also less common, heretofore reported only from early Miocene to early Pliocene sedimentary rocks of the southern Caribbean, Mexico, and Chile (e.g., BOSE, 1906; JUNG, 1965; FRASSINETTI & COVACEVICH, 1981; see Figure 1). This paper reports the first discovery of *A. nobilis karsteni* from Plio-Pleistocene sediments and in modern shelf environments of western tropical America.

In 1981 and 1982 the author found several partial molds of the "karsteni" form in gravelly-shelly sandstones near the base of the Mancora Tablazo sequence in northwestern Peru and in overlying siltstones of the same sequence

(Figure 1). These deposits were first described in some detail by BOSWORTH (1922), and lately have been re-examined by DEVRIES (1982, and in preparation), the latter author attributing the coarse and fine sediments, respectively, to semi-protected inlet and deep lagoonal environments.

Numerous specimens of *Architectonica nobilis karsteni* were recently recognized by the author among the collections of *A. nobilis nobilis* housed at the Los Angeles County Museum of Natural History (LACM). This material was collected live from midshelf depths between Baja California and Ecuador by the R/V *Anton Bruun* and other vessels (Figure 1). A consideration of the taxonomy of these specimens of *A. nobilis karsteni* is presented below, followed by a discussion of the ecological data available for fossil and modern occurrences. It will be argued that the longevity of the "karsteni" form, its morphological and ecological integrity, and possible European ancestry, together suggest the propriety of full specific rank for this taxon, herein identified as *Architectonica (Architectonica) karsteni* (Rutsch, 1934).

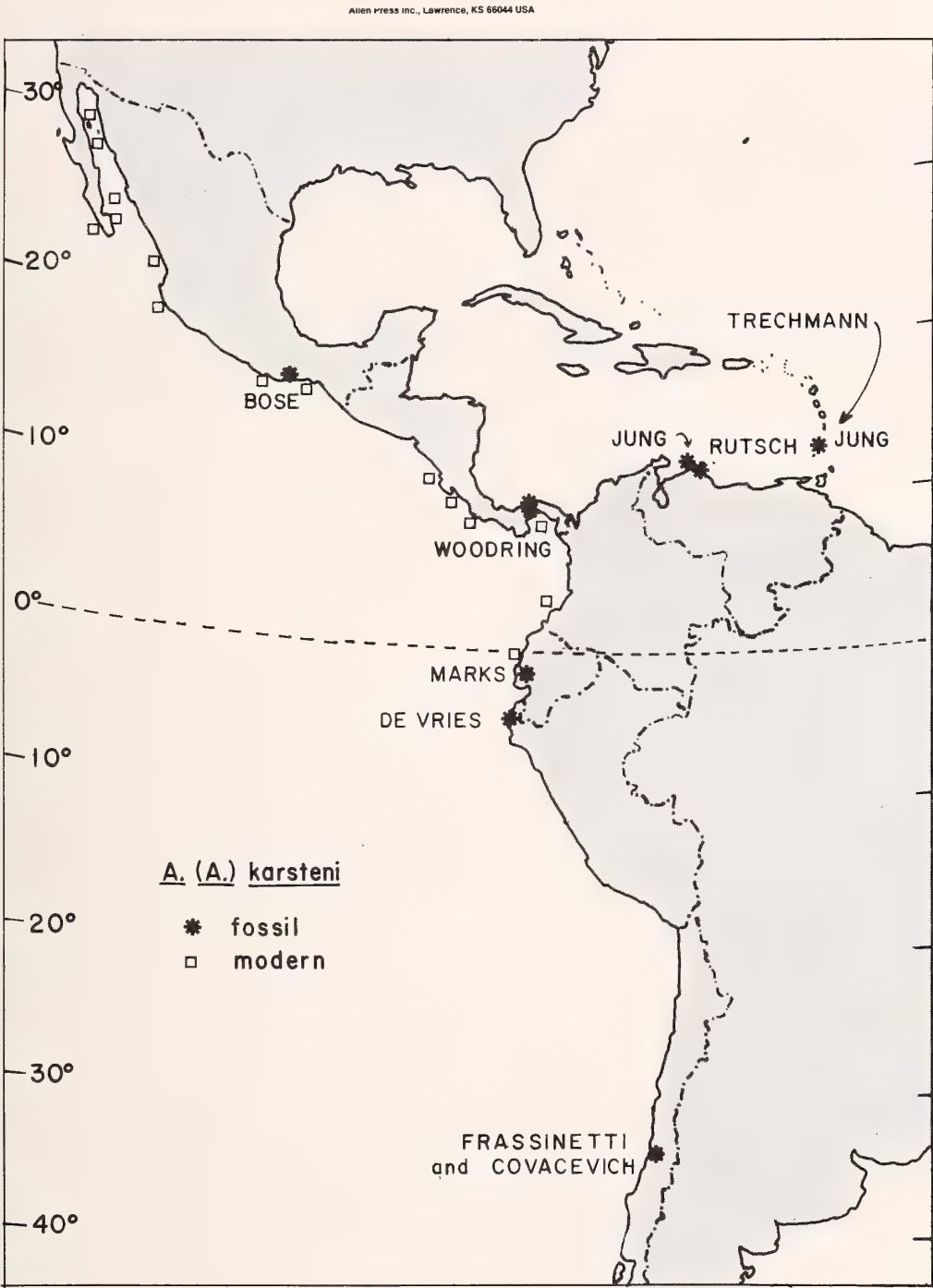


Figure 1

Neogene and Recent distribution of *Architectonica* (*Architectonica*) *karsteni* (Rutsch). Each fossil locality is designated by the author of the record.

TAXONOMY

Class Gastropoda

Subclass Prosobranchia

Order Mesogastropoda

Superfamily Architectonicacea

Family Architectonicidae Gray, 1850

Subfamily Architectonicinae Gray, 1850

Diagnosis: "Mainly heavy and solid species, 30–70 mm max. diam., a few as small as 7.5 mm. Single peripheral keel. Sculpture of strong cords and grooves, granose, tessellated or almost smooth. Umbilicus wide and perspective to narrow. Operculum chitinous, thin and flat" (GARRARD, 1977:510).

Genus *Architectonica* Röding, 1798Subgenus *Architectonica* Röding, 1798

Type species: By subsequent designation (GRAY, 1847: 151), *Trochus perspectivus* Linné, 1758.

Diagnosis: "Large to very large, medium to low conical; medium to wide perspective umbilicus; strong peripheral keel separated by a deep groove from both a dorsal and basal cingulum; usually both axially and spirally grooved and beaded, especially in early whorls; flat horny operculum . . ." (GARRARD, 1977:510).

Architectonica (*Architectonica*) ***karsteni***
(Rutsch, 1934)

Figures 2–12, 15, 16, 18, 20

Architectonica nobilis karsteni RUTSCH, 1934:44, pl. 1, figs. 8–10.

Architectonica sexlinearis haughti MARKS, 1951:93, pl. 2, figs. 2, 6.

Architectonica (*Architectonica*) *nobilis karsteni* Rutsch, 1934. WOODRING, 1959:167–168, pl. 30, figs. 1–3; JUNG, 1965: 488–489, pl. 64, figs. 8–10; JUNG, 1971:177, pl. 6, figs. 5, 6; FRASSINETTI & COVACEVICH, 1981:149–152, figs. 2a–2c.

Architectonica (*Architectonica*) *nobilis* subsp. WOODRING, 1973: 473, pl. 71, figs. 4, 5, 10, 11.

Solarium gatunense TOLA, 1908. TRECHMANN, 1935:549, pl. 21, figs. 21, 22.

[non] *Solarium gatunense* TOLA, 1908:692–693, pl. 25, fig. 3 (= *Architectonica nobilis* Röding, 1798).

Solarium villareloi BOSE, 1906 (in part):30–31, pl. 3, figs. 6, 7.

Original description: Shell rather low-spined; base strongly convex; umbilicus narrow. Base ornamented completely differently than *Architectonica nobilis*: on the keel, which surrounds the umbilicus, a deep wide furrow follows outward and after that a wide zone with strong radial folds. The two (up to three) granular spiral cords that characterize *A. nobilis* are missing. Before the peripheral

keel lies a partly granular spiral cord. The strong spiral thread that lies between both of these cords of the type specimen of *A. nobilis* is also missing . . . (free translation from original German description of RUTSCH, 1934).

Type locality: Punta Gavilan, northern Venezuela ("Cantaure" Formation, Miocene; RUTSCH, 1934).

Location of type: Museum of Basel, Holotype 142/1769, Museum No. 13.

Additional material: LACM 66-198. Four specimens from R/V *Anton Bruun* cruise 18B, Station 778, 93 m, W of Cabo Pasado, Ecuador (00°21'S, 80°41'W) collected live. LACM collections contain other specimens of *A. karsteni* whose distributions are illustrated in Figures 1 and 22.

OSU 36792. External mold of umbilical region and portions of base. Detail is well-preserved in calcareous gravelly sand. Collected by T. DeVries in 1981 from near base of Mancora Tablazo section at Cabo Blanco, northwest Peru.

Supplementary description: LACM 66-198a, b, c, d. Small to moderate size (see Table 1), only moderately thick, conical; umbilical width about $\frac{2}{5}$ total diameter. Protoconch not visible; teloconch with 7 whorls. Dorsal sculpture one narrow, flattened, peripheral cord and four wider cords, all granulose in early whorls, becoming smooth or nearly smooth on body whorl; cords bear minute spiral striae and on the two abaxial dorsal cords, a single weak spiral groove; grooves between dorsal cords narrow, usually $\frac{1}{5}$ to $\frac{1}{6}$ as wide as adjoining cords. Ventral sculpture consists of umbilical cord with numerous blunt rectangular nodes; adjoined peripherally by wide, deep, flat-bottomed groove. A sharply rounded spiral cord and spiral thread lie adjacent to peripheral dorsal cord. Intervening ventral area convex, crossed by radially splayed wrinkles that gradually fade peripherally; wrinkles intersected by 6 weakly developed spiral grooves and numerous minute spiral striae. Weak parietal groove emerges on columellar lip $\frac{1}{3}$ the distance abapically from the edge of succeeding whorl to the siphonal canal; a second weaker groove is present anteriorly. Color uniformly pale brown with radially directed bands of rectangular brown spots on dorsal cords and discontinuous thin spiral bands of brown on ventral side. Thin brown periostracum. Flat, chitinous operculum.

OSU 36792. Moderate size (27 mm diameter); umbilical cord with large rectangular nodes; bound peripherally by a single wide, deep, flat-bottomed spiral groove. Radially splayed, well-defined wrinkles, fading peripherally; single spiral cord against peripheral cord without intervening spiral thread. Ventral area with 4, possibly 6, weak spiral grooves passing between wrinkles.

Stratigraphic and geographic distribution: Northern Venezuela, middle Miocene (RUTSCH, 1934; JUNG, 1965); Carriacou (eastern Caribbean), late early-middle Mio-

cene (TRECHMANN, 1935; JUNG, 1971); Panama, early Miocene–early Pliocene (WOODRING, 1959, 1973); northern Colombia, Miocene (J. W. Durham, personal communication, 1984); Ecuador, middle Miocene (MARKS, 1951), upper Miocene (Olsson, unpublished USNM material, USGS Locality 23491); central Chile, early–middle Miocene (FRASSINETTI & COVACEVICH, 1981); southeastern Mexico, (?) early Pliocene (BOSE, 1906; J. W. Durham, personal communication, 1984); northwestern Peru, late Pliocene–early Pleistocene; Gulf of California to Ecuador, Recent (Figure 1, Table 2).

DISCUSSION

Although similar, *Architectonica karsteni* and *A. nobilis* may be distinguished by several important morphologic features, the most obvious being the absence ventrally of both a second strongly noded spiral cord and a second deep spiral groove on *A. karsteni* (see FRASSINETTI & COVACEVICH, 1981). Other spiral grooves do appear on the ventral face of *A. karsteni*, but these in no way resemble the deep grooves of either species (see Figures 5, 13). The latter are wide and squarely cut with a flat bottom. The former are usually narrow, shallow, and V-shaped. Significant gradations between these two groove forms are rarely seen in the Recent material from LACM collections and apparently never found in fossil specimens.

Most specimens of Recent *Architectonica karsteni* are thinner-shelled, lower-spired, more convexly rounded dorsally and ventrally, less granulose, and more uniformly colored in drab brown than *A. nobilis*. Dorsally, spiral grooves are narrower in *A. karsteni*; in *A. nobilis*, any of

the dorsal grooves may be nearly half as wide as the adjacent cords.

The spiral thread situated between the dorsal peripheral cord and the ventral cord near the periphery is present to some degree in all Recent specimens of *Architectonica karsteni*, as are all four dorsal grooves. In these two respects they resemble *A. nobilis* more than fossil *A. karsteni*, which usually lack the spiral thread and one or two of the dorsal grooves.

The columellar lip of all *Architectonica karsteni* is quite different from that of *A. nobilis*. The latter has a well-developed groove only one-fourth to one-fifth the columellar lip length below the superseding whorl, rather than one-third as in *A. karsteni* (Figures 16, 18–21). Anteriorly, the columellar lip of *A. nobilis* bears several tiny pleats and grooves that are not present in *A. karsteni*.

Specimens of *Architectonica karsteni* from Panama (WOODRING, 1959) and Ecuador (MARKS, 1951) were examined and compared with the newly discovered specimens (Table 1). Dorsally, fossils from both localities were somewhat less granulose and lacked one of four dorsal grooves. Ventrally, the Panama specimens (USNM 562636) lacked the incipient spiral grooves present across the entire base of the Recent specimens, but in the Ecuadorian specimens these nascent grooves (four in number) were readily visible. Undescribed upper Miocene *A. karsteni* from Ecuador collected by Olsson and housed at the U.S. National Museum (USGS Locality 23491) even display a third, thin spiral thread near the periphery as is seen on Recent specimens.

A close examination of the figure of *Solarium gatumense* TOULA (1908) reveals two deep grooves encircling the um-

Explanation of Figures 2 to 14

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Figures 2 to 12. *Architectonica (Architectonica) karsteni* (Rutsch, 1934).

Figure 2. LACM 66-198d. Recent, 93 m, off Cabo Pasado, Ecuador. Dorsal view. (×1.67).

Figure 3. LACM 66-198b. Recent, 93 m, off Cabo Pasado, Ecuador. Dorsal view. (×1.67).

Figure 4. LACM 66-198c. Recent, 93 m, off Cabo Pasado, Ecuador. Dorsal view. (×1.67).

Figure 5. LACM 66-198d. Ventral view. (×1.67).

Figure 6. LACM 66-198b. Ventral view. (×1.67).

Figure 7. LACM 66-198c. Ventral view. (×1.67).

Figure 8. LACM 66-198d. Apertural view. (×1.67).

Figure 9. LACM 66-198b. Apertural view. (×1.67).

Figure 10. LACM 66-198c. Apertural view. (×1.67).

Figure 11. OSU 36792. Late Pliocene–early Pleistocene, base of Mancora Tablazo sequence, Cabo Blanco, Peru. Latex cast of partially preserved ventral surface and umbilicus. (×1.4).

Figure 12. OSU 36792. Original sandstone mold from which latex cast (Figure 11) was made. (×1.4).

Figures 13 and 14. *Architectonica (Architectonica) nobilis* Röding, 1798.

Figure 13. LACM AHF-93839. Recent, Costa Rica. Ventral view showing two deep spiral grooves encircling umbilicus. (×1.81).

Figure 14. LACM AHF-93839. Dorsal view showing wide dorsal spiral grooves. (×1.81).



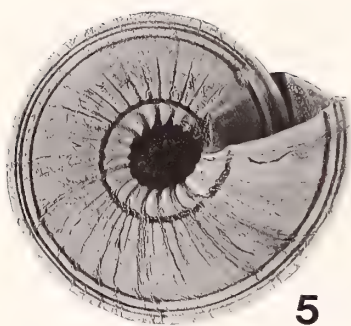
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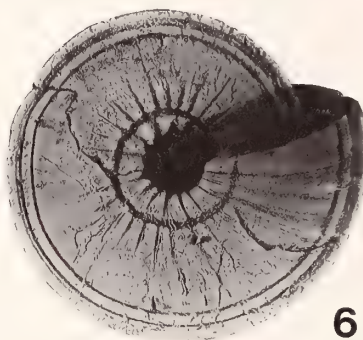
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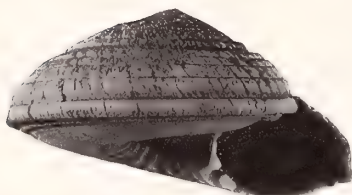
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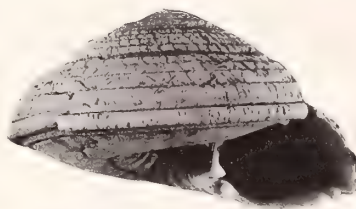
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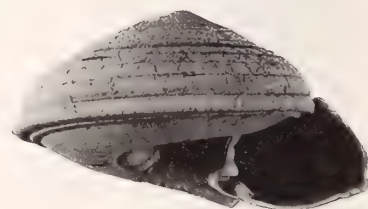
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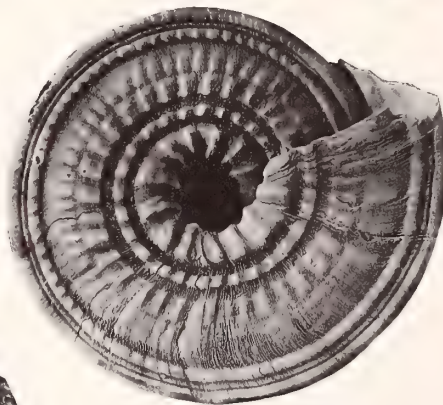
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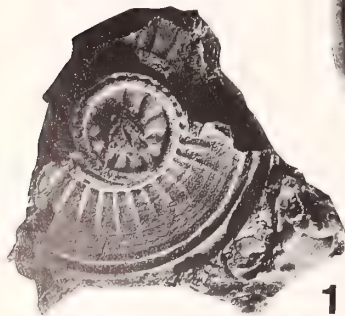
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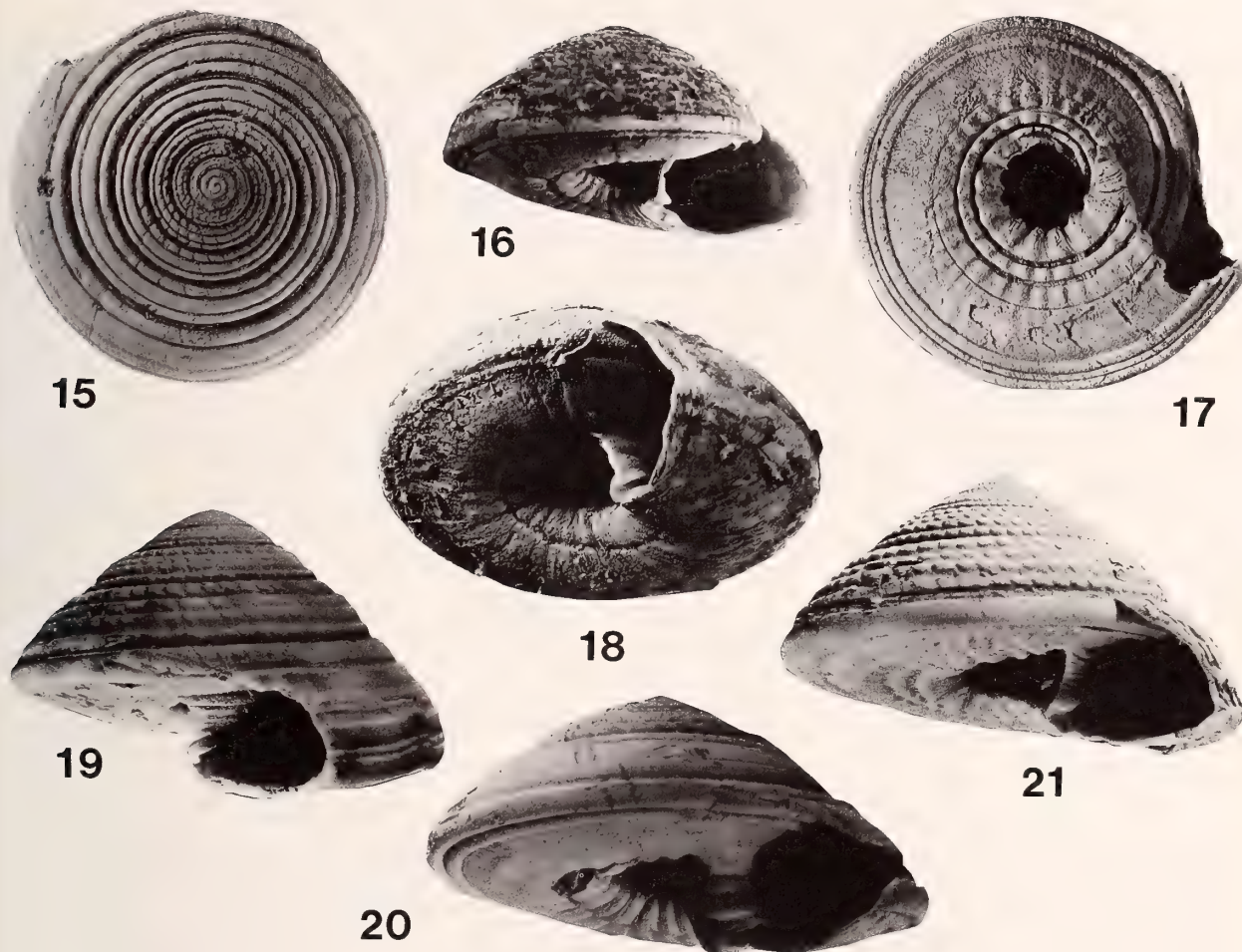
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Explanation of Figures 15 to 21

Figures 15, 16, 18, and 20. *Architectonica (Architectonica) karsteni* (Rutsch, 1934).

Figure 15. PRI 20444 (= *A. sexlinearis haughti* Marks, 1951). Middle Miocene, Daule Formation, Ecuador. Dorsal view. Note presence of only three dorsal grooves on younger whorls. ($\times 1.46$).

Figure 16. LACM 66-198a. Recent, 93 m, off Cabo Pasado, Ecuador. Lateral view of columella showing position of principal adapical groove and weaker grooves abapically on the columellar lip. ($\times 1.45$).

Figure 18. LACM 66-198a. Oblique apertural view of columella. ($\times 1.45$).

Figure 20. USNM 562636. Miocene, Panama. Oblique apertural view of columella showing position of adapical groove and absence of pleating on columellar lip. ($\times 1.75$).

Figures 17, 19, and 21. *Architectonica (Architectonica) nobilis* Röding, 1798.

Figure 17. OSU 36794. Late Pleistocene, Lobitos Tablazo, northwestern Peru. Ventral view showing two strong grooves bordering the umbilicus. ($\times 1.75$).

Figure 19. OSU 36793. Recent, northwestern Peru. Apertural view showing pleated columellar lip.

Figure 21. LACM AHF-93839. Recent, Costa Rica. Apertural view showing position of columellar adapical groove and pleated columellar lip. ($\times 1.81$).

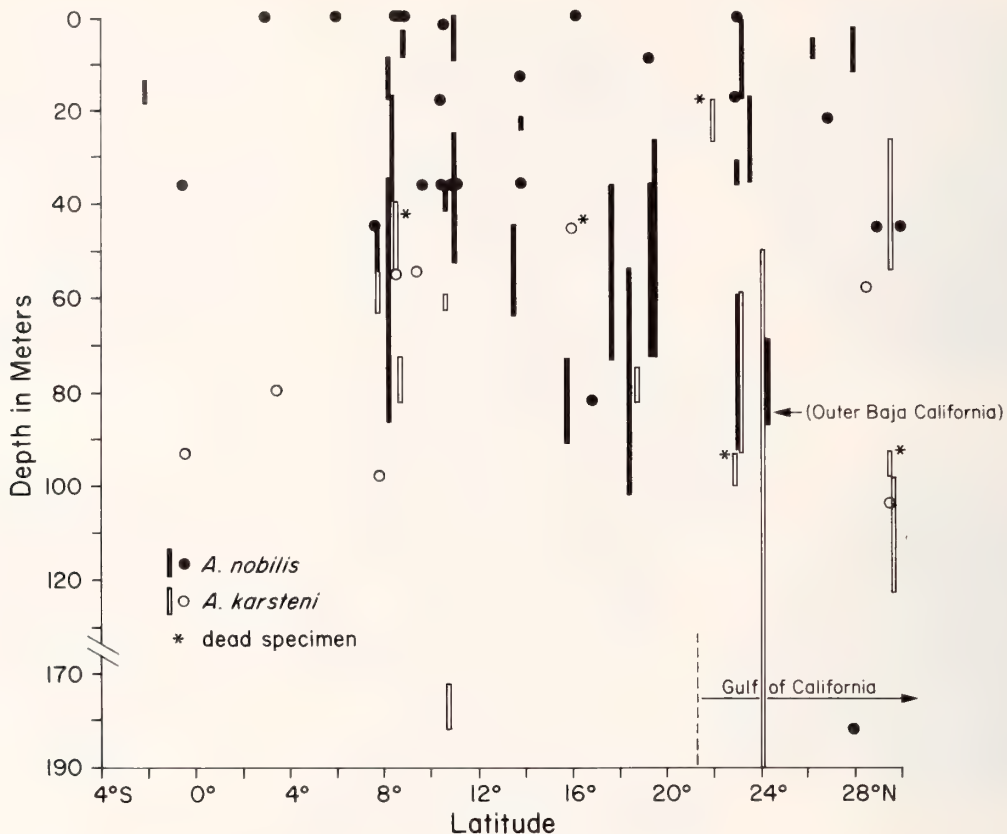


Figure 22

Latitudinal and bathymetric distribution of Recent *Architectonica* (*Architectonica*) *karsteni* (Rutsch). Data from collections of LACM; material collected by R/V *Anton Bruun* and other vessels.

bilicus. Thus, Toulou's specimen is properly referred to *Architectonica nobilis*. TRECHMANN (1935) was correct in not assigning his Caribbean specimen to *A. nobilis*; when referring it to *S. gatunense*, he probably was unaware of RUTSCH's (1934) year-old description of *A. karsteni*.

As noted by RUTSCH (1934), *Architectonica karsteni* bears a strong resemblance to European Miocene species of the same subgenus, particularly *A. grateloupi* (d'Orbigny, 1852) (COSSMANN, 1915:164, pl. 6, figs. 40, 41, 42), *A. carocollatum* (Lamarck, 1822), and varieties of the latter (SACCO, 1892:40-41, pl. 1, fig. 35; STRAUZ, 1966: 115-116, pl. 52, figs. 5, 7-10). *Architectonica grateloupi* is less granulose than Recent *A. karsteni* but no less granulose than many fossil *A. karsteni*. Four dorsal cords are present on all whorls, as in Recent *A. karsteni*. The umbilicus is somewhat wider than in any *A. karsteni*. *Architectonica grateloupi* typically has not one, but two ventral spiral threads adjacent to the dorsal peripheral cord.

Architectonica carocollatum and *A. carocollatum* var. *palatinum* (STRAUSZ, 1966) are also less granulose than Recent *A. karsteni*. Dorsal grooves are variably developed. On the typical form of *A. carocollatum* only two of four grooves are carried forward to the penultimate and ultimate whorls. On the "*palatinum*" form, never more than two dorsal grooves are present on any whorl.

Considering the specificity of the characters pertaining to *Architectonica karsteni* in Recent populations and the rarity of gradations in character with *A. nobilis*, the persistence of these characters through 20 million years, the widespread geographic range of the "*karsteni*" form, past and present, and the ecological arguments presented below, it is concluded that *A. (A.) nobilis karsteni* should be elevated to specific status.

Despite some morphological overlap between Recent *Architectonica karsteni* and *A. nobilis*, there is no reason that *A. karsteni* must be considered a New World Neo-

Table 1

Dimensions of selected *Architectonica* specimens, including specimens of *A. karsteni* illustrated in this paper.

Specimen	Diameter (mm)	Height (mm)	H/D	Umbilical width (mm)	UW/D
<i>Architectonica karsteni</i>					
LACM 66-198a	33.5	21.4	0.64	12.6	0.38
LACM 66-198b	28.5	16.8	0.59	9.7	0.34
LACM 66-198c	28.0	15.6	0.56	10.0	0.36
LACM 66-198d	27.8	16.0	0.58	9.7	0.35
OSU 36792	27	?	—	11.2	0.40
USNM 562636	37	19	0.5	14	0.4
SGOP 13122	24.8	14.1	0.57	9.3	0.37
PRI 20443	19.9	12.5	0.63	6.9	0.35
PRI 20444	35.2	23.7	0.67	13.3	0.38
<i>Architectonica nobilis</i>					
AHF 939-39	38.2	24.1	0.63	14.9	0.39
OSU 36793	37.0	23.2	0.63	14.9	0.39
OSU 36794	31.0	16.4	0.53	10.9	0.35

gene descendant of *A. nobilis*, given the ubiquity of forms very similar to *A. karsteni* throughout the Miocene of Europe.

ECOLOGICAL CONSIDERATIONS

Most Recent specimens of *Architectonica karsteni* in the LACM collection were recovered from depths in excess of 50 m, whereas *A. nobilis* was usually found at lesser depths (Figure 22). Only along the narrow continental shelf between 16 and 24°N was *A. nobilis* common at depths greater than 50 m.

Most fossil specimens of *Architectonica karsteni* were probably deposited in an offshore setting (Table 2). Fossil *A. nobilis* occur in the same strata as *A. karsteni*, as well as in adjacent strata. There is no evidence that these occurrences in other strata are from solely nearshore sediments. Thus, the apparent modern segregation of the two species by water depth cannot be demonstrated for the fossil record. Nonetheless, there is little basis for believing that *A. karsteni* was ever a regular inhabitant of very shallow water.

The 50-m break in the Recent distribution of the two

Table 2

Sedimentological information pertaining to Neogene and Recent occurrences of *Architectonica* (*Architectonica*) *karsteni* (Rutsch).

Locality	Formation	Sedimentology	Age	Author
Punta Gavilan, n. Venezuela	"Cantaure" Fm.	Glauconite, limonitic sandy limestone	Miocene	RUTSCH, 1934
Paraguana Peninsula, n. Venezuela	"Cantaure" Fm.	60% clay; thin-bedded sandstone; thin-bedded limestone; 30 m above bedrock	middle Miocene	JUNG, 1965
Carriacou, Grenadine Islands	Grand Bay Fm.	Ashy shale, fine agglomerates; hermatypic and ahermatypic corals	middle Miocene	TRECHMANN, 1935; JUNG, 1971
Carriacou, Grenadine Islands	Kendace Fm.	Calcareous marls	late early Miocene	JUNG, 1971
Panama	La Boca Fm.	Silty or tuffaceous mudstone; minor conglomerate; coralline limestone	early Miocene	WOODRING, 1973
Panama	Chagras Fm.	Massive fine sandstone and siltstone; overlies barnacle coquina	late Miocene-early Pliocene	WOODRING, 1959
Daule Basin, Ecuador	Daule Fm.	Blue siltstone	middle Miocene	MARKS, 1951
Punta Perro, c. Chile	La Navidad Fm.	Coarse quartz sandstone	early-middle Miocene	FRASSINETTI & COVACEVICH, 1981
Tuxtepec, Mexico	—	Poorly consolidated sands	Pliocene	BOSE, 1906
Cabo Blanco, Peru	Mancora Tazobazo beds	Calcareous, gravelly sandstone	late Pliocene-early Pleistocene	This paper
Ecuador to Gulf of California; Baja California Sur	—	Gravel; mud; fine sand; shells	Recent	This paper

Architectonica species in the eastern tropical Pacific Ocean is approximately coincident with the lower boundary of the permanent oceanic thermocline (e.g., PATZERT, 1978). Water temperatures immediately beneath the thermocline fluctuate seasonally but are generally several Centigrade degrees cooler than surface waters. Given that the isotherms at 50–100 m (within the depth range of *A. karsteni*) extend several latitudinal degrees beyond the poleward limits of the geographic range of *A. karsteni*, it would seem that this species is not making full use of its thermally defined habitat. Hence, geographic and bathymetric restraints on its distribution cannot be principally thermal. Nor does the restraint appear to be sedimentological, as live specimens of *A. karsteni* were dredged from all types of substrate. Factors not considered here, including competition, seasonal temperature changes interacting with the life history of the species, and circulation patterns, may exert more control on the distribution of this species.

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The *Stenoplax limaciformis* (Sowerby, 1832) Species Complex in the New World (Mollusca: Polyplacophora: Ischnochitonidae)

by

ROBERT C. BULLOCK

Department of Zoology, University of Rhode Island, Kingston, Rhode Island 02881

Abstract. The systematic status of species traditionally associated with the *Stenoplax limaciformis* species complex of the New World has remained controversial. The group is reviewed and four sibling species are recognized on the basis of differences in shell sculpture, radular morphology, and esthete pore density: *Stenoplax limaciformis* (Sowerby, 1832) from the tropical eastern Pacific, *S. purpurascens* (C. B. Adams, 1845) from the West Indies and northern South America, *S. floridana* (Pilsbry, 1892) from the Florida Keys south to Colombia, and a long-neglected species, *S. producta* (Reeve, 1847), from the Bahama Islands, Cuba, Jamaica, and Hispaniola south to Honduras and Isla de San Andrés. Two distinct lineages are recognized within the sibling group: (1) *S. floridana* and *S. producta* from the western Caribbean and (2) the West Indian *S. purpurascens* and the eastern Pacific *S. limaciformis*. The restricted distribution of the Caribbean species within the West Indian Faunal Province, which is assumed to be a result of a very brief free-swimming larval stage, the insular environment of the area, and ocean current patterns, lends support to the theory of paraprovincialism as applied to the Caribbean. *Stenoplax floridana* and *S. producta* exhibit a Caloosahatchian distributional pattern, while *S. purpurascens* reflects a Gatunian origin.

INTRODUCTION

THE CONFUSING nomenclatural history of *Stenoplax limaciformis* (Sowerby, 1832) and the related nominal species *S. purpurascens* (C. B. Adams, 1845) and *S. floridana* (Pilsbry, 1892) has been presented by KAAS (1972) and FERREIRA (1978). Taxonomic problems exist due to limited material available for study, intraspecific variability, and the small, but consistent, differences exhibited by these species. The untrained eye, even with the aid of a dissecting microscope, may not easily differentiate the species of *Stenoplax*.

During the first half of this century two species within the *Stenoplax limaciformis* group were recognized: *S. limaciformis* from the eastern Pacific and the West Indies, and *S. floridana* from the Florida Keys. KAAS (1972), on the basis of limited and poorly preserved material, concluded that the West Indian populations of "*limaciformis*" represent a distinct species, *S. purpurascens*. ABBOTT (1974) recorded all three species from Florida and the West Indies. After an examination of large samples of these nominal species, FERREIRA (1978) concluded that all of these

Stenoplax "species" are, in fact, a single biological species. In the most up-to-date listing of Recent polyplacophoran species, KAAS & VAN BELLE (1980) supported Ferreira in part, and they synonymized *S. purpurascens* with *S. limaciformis*; however, they retained *S. floridana* as a distinct species. I will show in the present study that the *S. limaciformis* complex must be considered as a group of sibling species. Each of the previously mentioned species is specifically distinct and, furthermore, a fourth species, *S. producta* (Reeve, 1847), also exists in the Caribbean region.

MATERIALS AND METHODS

Specimens from the Museum of Comparative Zoology (Cambridge), the Florida Department of Natural Resources Marine Research Laboratory, and the personal collections of G. T. Watters (Ohio State University) and the author were examined in detail. Other material was available due to the kindness of A. Solem of the Field Museum of Natural History, T. Hopkins and D. Blizzard of the Dauphin Island Sea Lab, J. Brooks, D. Dexter, D.

Holt, A. Martins, and T. Spight. Photographs of previously examined type material in the British Museum (Natural History) and the Museum National d'Histoire Naturelle, Paris, were available for study.

Only non-eroded specimens were used for the various aspects of this study. Dry specimens most easily revealed the small sculptural features necessary for species determination; preserved or living specimens were blotted with an absorbent wipe to remove surface liquid.

The shell-plates (valves) of many individuals were disarticulated and cleaned using a 2 N solution of KOH. Specimens to be studied using scanning electron microscopy (SEM) were further cleaned in heated KOH solution and then placed in a series of distilled water rinses during which they were ultrasonically cleaned. The valves were then mounted on aluminum specimen stubs using Duco cement and wedges of aluminum foil. After coating with carbon and gold/palladium in a Denton DV-502 vacuum evaporator, the samples were studied using an ISI SEM model MSM-3, located in the Department of Zoology at the University of Rhode Island.

Examination of numerous SEM photographs revealed apparent differences in esthete pore density that showed promise for phylogenetic studies. For this part of the investigation a total of 41 individuals was selected at random. Examples of *Stenoplax limaciformis* came from Mexico ($n = 3$) and Panama ($n = 10$); *S. purpurascens* from Puerto Rico ($n = 1$), the Dominican Republic ($n = 1$), Barbados ($n = 1$), Aruba ($n = 1$), and Panama ($n = 7$); and *S. floridana* from the Florida Keys ($n = 8$), Honduras ($n = 1$), and Panama ($n = 2$). For each individual, SEM photographs of an intermediate valve were made of the top central area (TC), anterior margin (AM), and lateral triangle (LT). Each photograph covered 0.145 mm^2 of the shell surface. Surface area measurements and esthete pore counts were taken from $20.3 \times 25.4 \text{ cm}$ photographic enlargements. In all TC calculations any portion of the lateral triangle that was visible was excluded from consideration. All area measurements were made using a K & E compensating polar planimeter. In order to ascertain the phylogenetic usefulness of these data, percent rib area (PCTRA), a measure of rib prominence, was plotted against micropore density (SDEN), megalopore density (LDEN), and total pore density (TOTDEN) for each area of the valve. It was evident that LDEN, which represents the density of megalesthetes, was a more meaningful character than SDEN due to the high degree of variability in the number of microesthetes associated with each megalesthete. Further analyses involved only LDEN for the three areas of the intermediate valve combined.

Canonical variate analysis, using LDEN and PCTRA as variables, was employed in order to examine the differences between the species that were established *a priori* on the basis of general shell and radular features. Mahalanobis D^2 distances were calculated for each pair of species. In canonical variate analysis, variables are transformed to maximize differences between *a priori* groups

relative to within group variation (NEFF & MARCUS, 1980; CAMPBELL & ATCHLEY, 1981). This form of analysis has been shown to be an invaluable tool in the analysis of variation between populations, groups of populations, and species. All computations were carried out using the SAS program at the Academic Computer Center at the University of Rhode Island.

The valves selected for line drawings were taken from individuals used for SEM studies. These valves were mounted on large pins and coated with magnesium oxide in order to enhance sculptural detail.

Radulae and girdle elements were briefly examined using SEM techniques; however, most samples were more easily studied using light microscopy. Permanent microslide mounts were prepared by dehydrating in ethanol, clearing in toluene, and mounting in Canada balsam.

The radulae were excised, thoroughly cleaned, and teased apart before study. The many small differences noted in denticle cap morphology were best seen in an outline view of the cap; for each preparation a portion of the radula was teased apart enough to separate some denticle caps from major lateral teeth. In specimens that had been preserved for more than a few years, this posed no substantial problem because there was a tendency for the denticle caps to fall off during the cleaning stages. The caps, due to their magnetic property, were collected on the tip of an insect pin and transferred to the mounting medium. The radulae of 69 individuals were examined in detail by light microscopy (*Stenoplax limaciformis*, 6; *S. purpurascens*, 7; *S. floridana*, 29; *S. producta*, 27). The radulae of 139 other individuals were isolated, cleaned, and observed, but not mounted.

Girdle scales were studied using cleaned, isolated scales. Because of the great amount of variation between girdle scales, the marginal spicules, and the small ventral scales of the same specimen, preparations were made by taking a small sample (about a fourth of the animal length, on one side in the middle) and processing it as a unit. The scales often separated, especially during ultrasonic cleaning, but they were pipetted and transferred to a microslide using a small, disposable Pasteur pipet. The scales were allowed to settle in the pipet in order to concentrate them. The filmlike folded sheet of ventral scales and the remainder of the dorsal scales were then added to the slide before the Canada balsam was applied. The small, rectangular scales of the ventral surface of the girdle were so similar among the species examined that descriptions of them are not included in the present study. Therefore, all references to "girdle scales" refer to the dorsal scales and the outer fringe of spicules.

ABBREVIATIONS

The following institutions and individuals are cited in the text using the abbreviations listed below:

ANSP—Academy of Natural Sciences of Philadelphia
BLM—Bureau of Land Management

BMNH—British Museum (Natural History), London
 DISL—Dauphin Island Sea Lab, Alabama
 FDNR—Florida Department of Natural Resources Marine Laboratory, St. Petersburg
 FMNH—Field Museum of Natural History, Chicago
 GTW—Collection of G. T. Watters
 MCZ—Museum of Comparative Zoology, Cambridge
 MNHNP—Museum National d'Histoire Naturelle, Paris
 RCB—Collection of R. C. Bullock
 SDSC—San Diego State College

SYSTEMATIC SECTION

Family ISCHNOCHITONIDAE Dall, 1889

Subfamily ISCHNOCHITONINAE Dall, 1889

The systematics of polyplacophorans at the family and subfamily levels are greatly in need of revision. I follow the conservative approach presented by KAAS & VAN BELLE (1980), who included in the Ischnochitoninae the genera *Ischnochiton* Gray, 1847, *Stenoplax* Dall, 1879, *Stenochiton* H. Adams & Angas, 1864, *Lepidozona* Pilsbry, 1892, and *Connexochiton* Kaas, 1979. The only recent review of the subfamily is that of VAN BELLE (1977).

Genus *Stenoplax* (Carpenter MS) Dall, 1879

Type species: *Chiton limaciformis* Sowerby, 1832 by original designation.

There is a difference of opinion concerning the authorship of *Stenoplax* and other names proposed in the large unpublished chiton manuscript of P. P. Carpenter and later properly introduced by DALL (1879), PILSBRY (1892–1894), and others. SMITH (1960), KEEN (1971), FERREIRA (1978), and various west coast workers have consistently assigned authorship to Carpenter. DALL (1879) and PILSBRY (1892–1894) credited Carpenter where they took information directly from the manuscript. The manuscript, housed in the Division of Mollusks at the U.S. National Museum of Natural History, is in two large scrapbooks. Much of the writing is in curious shorthand. Given the condition of the manuscript, it seems to me incredible that Carpenter should be considered as having published these names in the meaning of the International Code of Zoological Nomenclature. I follow BOSS *et al.* (1968) and assign the authorship to the person who validly introduced the name in question.

The genus *Stenoplax* was introduced (DALL, 1879:78) on the same page as *Stenoradsia*. The latter name is currently accepted as a subgenus of *Stenoplax s.l.* (SMITH, 1961; VAN BELLE, 1977; KAAS & VAN BELLE, 1980). SMITH (1961) also listed *Stenochiton* Adams & Angas, 1864, as a subgenus of *Stenoplax*, but Australian workers (*cf.* ASHBY, 1918; IREDALE & HULL, 1927) and VAN BELLE (1977) have considered *Stenochiton* a separate genus. Should this genus of elongate, *Stenoplax*-like chitons be considered congeneric with *Stenoplax*, the name *Stenochiton* would have precedence.

When DALL (1879) introduced the genus *Stenoplax*, he listed the type species as "*S. limaciformis* Sby." It seems inconceivable that Dall, or Carpenter who had no doubt seen type specimens in the British Museum, could have misidentified such a well known species; but the only information presented by Dall, including his figure (pl. 2, fig. 13), does not coincide with features of *S. limaciformis* or any other *Stenoplax s.s.* Dall stated that the central tooth is very small and that the major lateral tooth has a simple cusp. In fact, all *Stenoplax s.s.* have a tricuspidate denticle cap (THIELE, 1893; TAKI, 1954; this paper), and the central tooth is moderately narrow but certainly not "small" as Dall stated. In spite of this discrepancy, the use of the name *Stenoplax* has not been questioned.

Stenoplax Dall *s.s.*

Description: Animal elongate, of medium size, reaching a length of about 50 mm. Color highly variable. Valves moderately flattened to inflated. Sculpture of anterior valve and posterior slope of posterior valve granular, nodulose, or of concentric ribs; in some forms the granules or nodules coalesce to form radial or concentric sculpture. Central areas and jugum with longitudinal ribs which may break up into pustules near the lateral triangle. Mucro of posterior valve central or posteriorly acentric. Slitting of insertion plates highly variable within each species; anterior valve with 8–14 slits, posterior valve with 7–12 slits; intermediate valves with one slit per side. Dorsal girdle scales very small, typically about 120 μ m high, 80 μ m wide, with 9–19 ribs per scale; ribs may or may not reach apex. Denticle cap of major lateral tooth tricuspidate.

Stenoplax s.s. includes: *S. limaciformis* (Sowerby, 1832) from the eastern Pacific; *S. purpurascens* (C. B. Adams, 1845), *S. floridana* (Pilsbry, 1892), and *S. producta* (Reeve, 1847) from the western Atlantic; and *S. venusta* (Is. & Iw. Taki, 1931) and *S. alata* (Sowerby, 1841) from the Indo-Pacific region. *Ischnochiton kempfi* Righi, 1971, from Brazil is also a *Stenoplax*, but KAAS & VAN BELLE (1980) considered it a member of the subgenus *Stenoradsia*; its relationship to *Stenoplax s.s.*, especially the *S. floridana*–*S. producta* lineage, needs to be investigated, but material is presently unavailable. Some other New World species may be properly placed in *Stenoplax s.s.* For example, *S. boogi* (Haddon, 1886) appears to be a *Stenoplax*, but it does not belong to the *S. limaciformis* group. ABBOTT (1974) included *Ischnochiton erythronotus* (C. B. Adams, 1845) in *Stenoplax*, but FERREIRA (1978) noted that this species is a junior subjective synonym of *Ischnochiton striolatus* (Gray, 1828) which is not considered a *Stenoplax*.

I have found that the girdle scales of *Stenoplax s.s.* polarize light. Whether there is any adaptive significance to this crystalline structure of calcium carbonate is unknown.

The biology of *Stenoplax s.s.* species is poorly known. Anatomical observations were reported by PLATE (1901) who studied *S. alata* from the Philippine Islands. It is generally thought that polyplacophorans are herbivorous

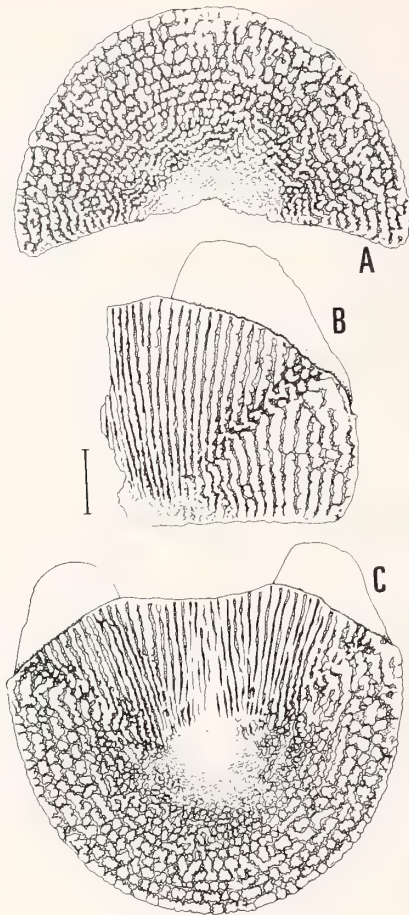


Figure 1

Stenoplax limaciformis (Sowerby). Punta Mala, Panama (RCB). A, anterior valve. B, right portion of intermediate valve. C, posterior valve. Scale bar = 1 mm.

(HYMAN, 1967), but some chitons are definitely omnivorous if not carnivorous (BARNAWELL, 1960; MCLEAN, 1962; Thorpe in KEEN, 1971). *Stenoplax* appears to fall into the latter category. PLATE (1901) found foraminiferans in the gut of *S. alata*. RAEIHLE (1967) reported that aquarium-kept *S. floridana* feed on mussel meat.

Stenoplax s.s. lives in a fairly restricted habitat. In a note on a label for *S. limaciformis*, a collector noted that it was found living "buried on sides of deeply bedded rocks." Caribbean species also live on rocks embedded in the substrate. In all cases, the rocks must actually be embedded, not just be resting on other rocks, and the substrate is usually clean, coarse sand or gravel. The species are absent in silty areas or in anaerobic substrates. Species of *Stenoplax s.s.* typically inhabit shallow waters from the low tide mark to a depth of a few meters. They are known to occur in deeper water as records from the western coast

of Florida and the Bahamas attest. RIGHI (1971) obtained specimens of *S. purpurascens* from as deep as 90 m.

Key to the species of the
Stenoplax limaciformis species complex

1. Ribs of central areas conspicuously broken into pustules near lateral triangle; lateral triangle usually granular *S. floridana*
Ribs of central areas forming few, if any, pustules; lateral triangle with concentric ribs which may be broken into broad nodules 2
2. Posterior valve elongate; mucro posteriorly accentric; microfurrows, visible under high magnification, in all grooves *S. producta*
Posterior valve not elongate; mucro centrally located; grooves smooth 3
3. Anterior valve and posterior slope of posterior valve with wavy, concentric ribs *S. purpurascens*
Anterior valve and posterior slope of posterior valve with nodular sculpture *S. limaciformis*

Stenoplax limaciformis (Sowerby, 1832)

(Figures 1–7, 8A, B, 9A)

Chiton limaciformis Sowerby in BRODERIP & SOWERBY, 1832: 26 (Inner Lobos Island in Peru and Guacomayo in Central America; holotype in BMNH); REEVE, 1847: pl. 8, sp. 42.

Chiton (Ischnochiton) limaciformis Sowerby. SHUTTLEWORTH, 1853:190.

Stenoplax limaciformis (Sowerby). DALL, 1879:78; KEEN, 1958:526, fig. 44; Thorpe in KEEN, 1971:871, sp. 24; ABBOTT, 1974 [in part]:396; FERREIRA, 1978 [in part]: 87; KAAS & VAN BELLE, 1980:74.

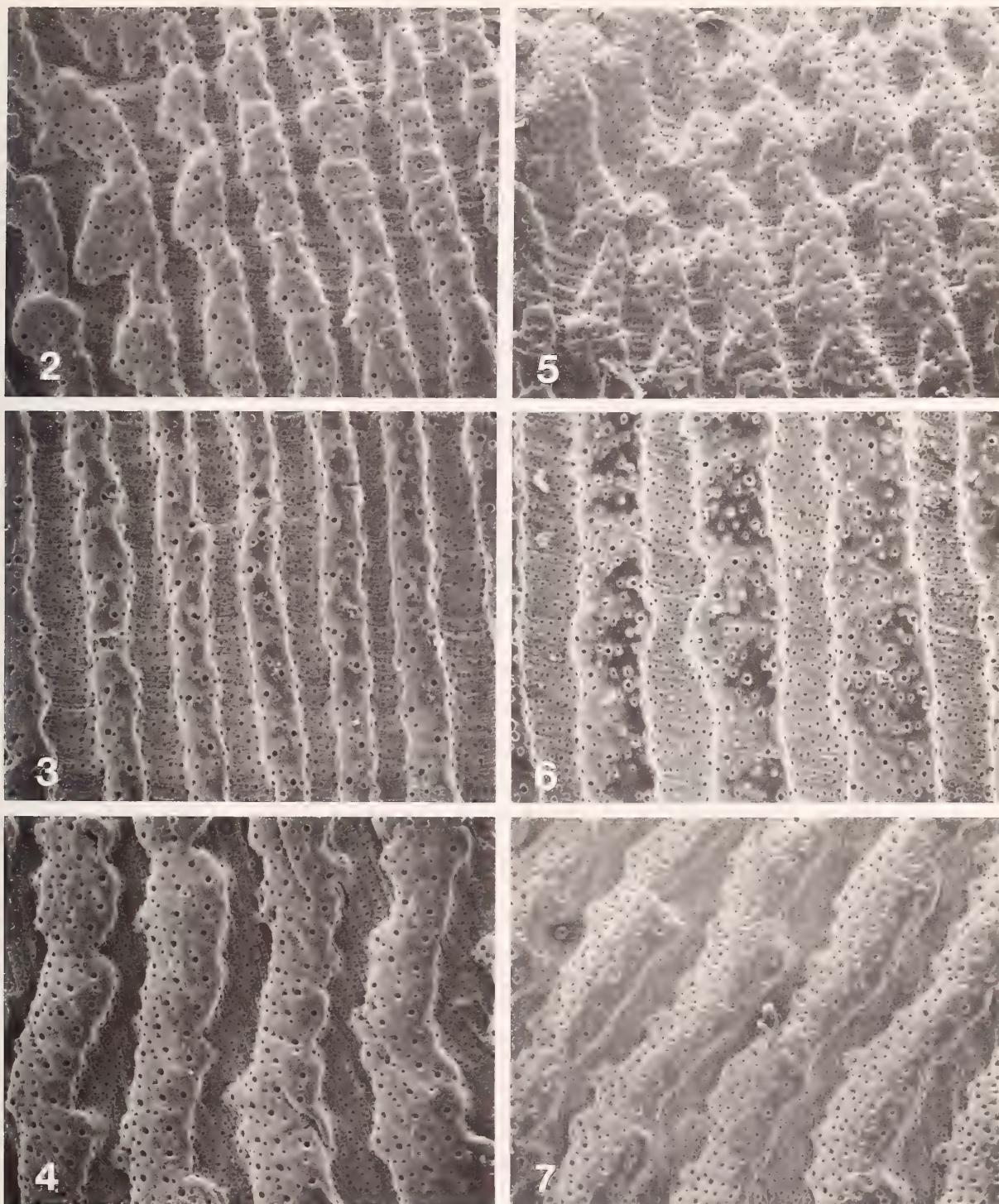
Ischnochiton (Stenoplax) limaciformis (Sowerby). PILSBRY, 1892:57, pl. 16, figs. 9–16.

Chiton angustus CLESSIN, 1904:120, pl. 41, fig. 1 (Central America; location of type unknown).

Ischnochiton limaciformis (Sowerby). PILSBRY & LOWE, 1932: 129; KAAS, 1972:71.

Description: Animal reaching a length of 45 mm, elongate. Anterior valve with concentrically arranged nodules, but occasionally nodules coalesce to form radially arranged groups of nodules; insertion plate with 9–13 slits. Intermediate valves rounded; longitudinal ribs of central area about as wide as intervening grooves and bend laterally; ribs become irregular near lateral triangle; ribs of jugum close-packed. Lateral triangle with broad close-packed concentric ribs which at times are broken to give a slightly nodular appearance. One slit per side in insertion plate. Posterior valve with central mucro; central areas with sculpture like that of intermediate valves; posterior slope sculpture similar to that of anterior valve; insertion plate with 7–12 slits.

Girdle scales slightly curved, variable in proportions, but typically about 102 μ m long, 87 μ m wide; 10–19 ribs per scale; ribs reach apex. Girdle fringe with straight, ribbed spicules, approximately 120 μ m in length.



Explanation of Figures 2 to 7

Scanning electron micrographs of intermediate valve sculpture of *Stenoplax limaciformis* (Sowerby). Posterior side toward top of page; all photographs 186 \times . Figures 2 to 4: Punta Mala, Panama (RCB). Figures 5 to 7: Acapulco, Mexico (MCZ 204170).

Figures 2, 5. Posterior region of central area near lateral triangle. Note the large number of esthete pores on the ribs, the lack of groove microsculpture, and that the ribs become irregular, but that they do not break into pustules.

Figures 3, 6. Central area near anterior margin.

Figures 4, 7. Lateral triangle.

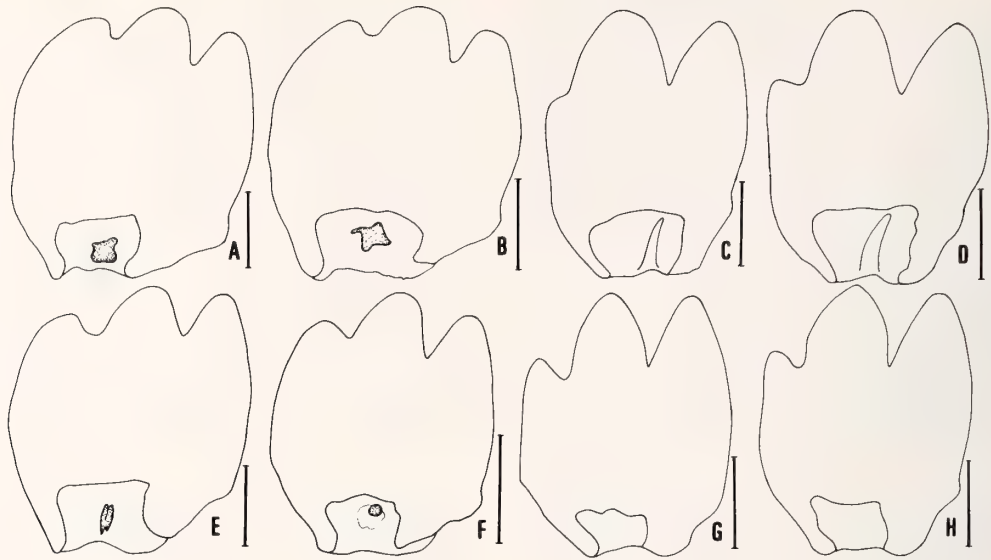


Figure 8

Representative denticle caps of the major lateral radular tooth of New World species of the *Stenoplax limaciformis* complex.

A and B, *S. limaciformis*: A, Playa Caleta, Acapulco, Mexico (RCB); B, Punta Mala, Panama (RCB).

C and D, *S. producta*: C, Anthonys Key, Roatán Id., Honduras (RCB); D, Harbour Island, Eleuthera, Bahama Islands (GTW).

E and F, *S. purpurascens*: E, Bridgetown, Barbados (RCB); F, North side of Galeta Id., Panama (RCB).

G and H, *S. floridana*: G, Verde Id., Mantilla Pt., Porto Bello, Panama (RCB); H, Indian Key Fill, Florida Keys, Florida (RCB). Scale bar = 50 μ m.

Radula typical for subgenus. Denticle cap of major lateral tooth tricuspidate, rather squat; small cusp moderately pronounced; side with small cusp swollen; brown basal spot present.

Remarks: *Stenoplax limaciformis* seems to be most closely related to *S. purpurascens*. Both species have blunt cusps and a brown basal spot on the denticle cap, and both exhibit rather broad ribs with many esthete pores on the central areas. Neither species has any break-up of the central area ribs into pustules. The more even, wavy, concentric ribs of the anterior valve and the posterior slope of the posterior valve separate *S. purpurascens* from *S. limaciformis*. The denticle caps of the two species are quite different: in *S. purpurascens* the small cusp is much more pronounced than in *S. limaciformis*, and the outline of the denticle cap on the side of the small cusp is never swollen as it always is in *S. limaciformis* (Figures 8A, B, E, F). For additional comments about the relationship between *S. limaciformis* and *S. purpurascens*, see the remarks for the latter species.

Distribution: *Stenoplax limaciformis* occurs from Puerto-citos and La Libertad, Mexico, south to Peru (Thorpe, in KEEN, 1971) (Figure 9A).

Specimens examined: *Mexico:* San Luis Gonzaga; Mazatlán (both MCZ); Isla Pajaros, Mazatlán (SDSC); Acapulco (MCZ, RCB).—*Costa Rica:* Playas del Coco [10°31'N, 85°43'W] (RCB).—*Panama:* Punta Mala; Naos Id.; Culebra Id.; W side of Taboga Id.; W side of Morro de Taboga, Taboga Id.; E side of Taboga Id., near Urava Id. (all RCB).

Stenoplax purpurascens (C. B. Adams, 1845)

(Figures 8E, F, 9A, 10–13)

Chiton purpurascens C. B. ADAMS, 1845:9 (Jamaica; holotype MCZ 155962); CLENCH & TURNER, 1950:334, pl. 42, fig. 2 [holotype figured].

Chiton sanguineus REEVE, 1847:pl. 17, sp. 98 (St. Vincent, W. Indies, holotype in BMNH).

Chiton (Ischnochiton) purpurascens C. B. ADAMS. SHUTTLEWORTH, 1853:199.

Onitochiton [sic] pruinosum ROCHEBRUNE, 1884:35 (Ile Cochino, Guadeloupe; type in MNHN).

Ischnochiton (Stenoplax) limaciformis (Sowerby). DALL, 1889:415 [in part]. *Non Stenoplax limaciformis* (Sowerby).

Ischnochiton limaciformis (Sowerby). PILSBRY, 1892:57 [in part]; DALL & SIMPSON, 1901:452; WARMKE & ABBOTT, 1961:217, text fig. 32e; RIGHI, 1971:126, figs. 13–18; GÖTTING, 1973:248, pl. 9, fig. 5; RIOS, 1975:265;

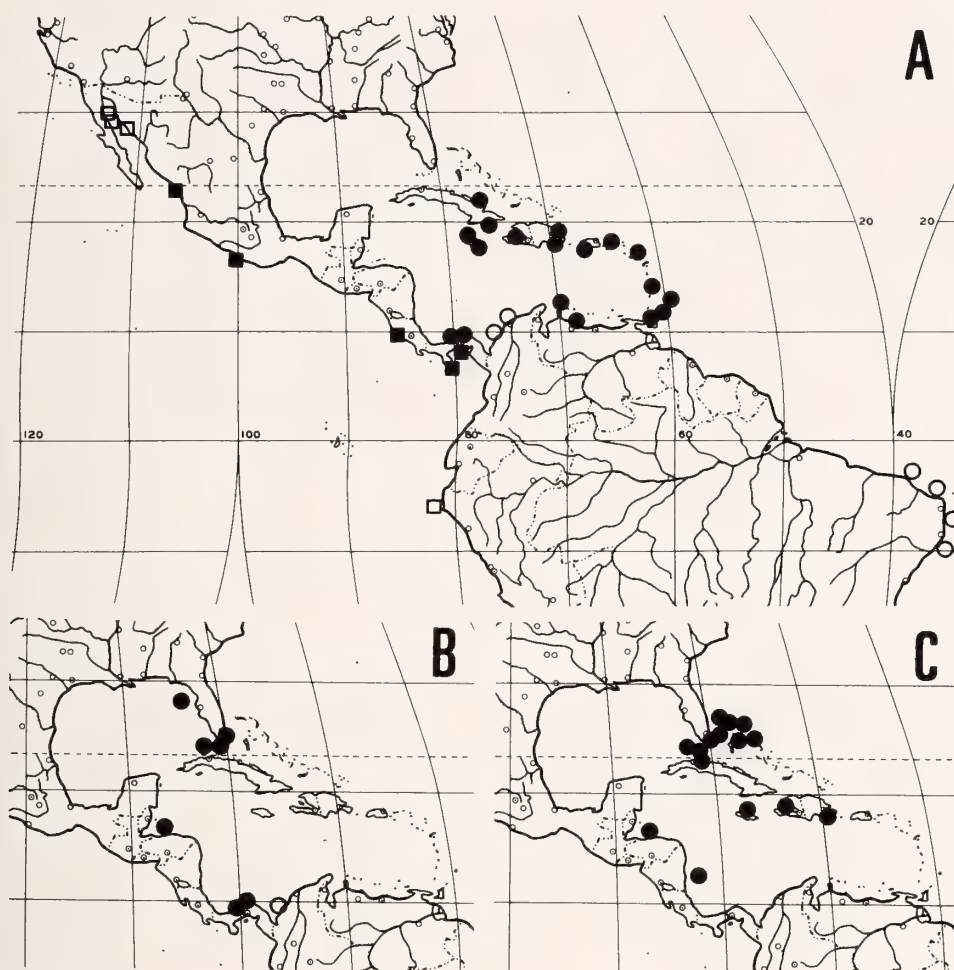


Figure 9

Known distribution of species of the *Stenoplax limaciformis* complex in the New World. A, *S. limaciformis* (■) and *S. purpurascens* (●). B, *S. floridana*. C, *S. producta*. Closed marks represent specimens examined; open marks indicate localities taken from the literature.

HUMFREY, 1975:290, fig. 18d. *Non Stenoplax limaciformis* (Sowerby).

Stenoplax producta (Reeve). THIELE, 1909:7. *Non Stenoplax producta* (Reeve).

Ischnochiton productus (Reeve). THIELE, 1910a:80; THIELE, 1910b:110. *Non Stenoplax producta* (Reeve).

Ischnochiton purpurascens (C. B. Adams). ABBOTT, 1954:320; ABBOTT, 1958:108.

Stenoplax purpurascens (C. B. Adams). ABBOTT, 1974:396 [erroneously reported from the Florida Keys and Bermuda].

Stenoplax limaciformis (Sowerby). FERREIRA, 1978 [in part]:87; KAAS & VAN BELLE, 1980 [in part]:74. *Non Stenoplax limaciformis* (Sowerby).

valves often streaked or speckled with darker or lighter colors. Anterior valve with broad, close-packed, wavy, concentrically arranged ribs; insertion plate with 9–13 slits. Intermediate valves somewhat flattened to quite inflated; ribs of central areas wider than intervening grooves and bend laterally; ribs becoming irregular, but not broken into pustules near lateral triangle; longitudinal ribs of jugum fine, close-packed, directed anteriorly; lateral triangle with broad, slightly oblique, concentric ribs; insertion plate with one slit per side. Posterior valve with central mucro; central areas with sculpture like that of intermediate valves; posterior slope with sculpture of lateral triangle, but slightly more irregular; insertion plate with 8–11 slits.

Girdle scales 120–150 μ m high, about 95 μ m wide; 15–

Description: Animal reaching a length of 45 mm, elongate. Color variable with pink or green predominating;

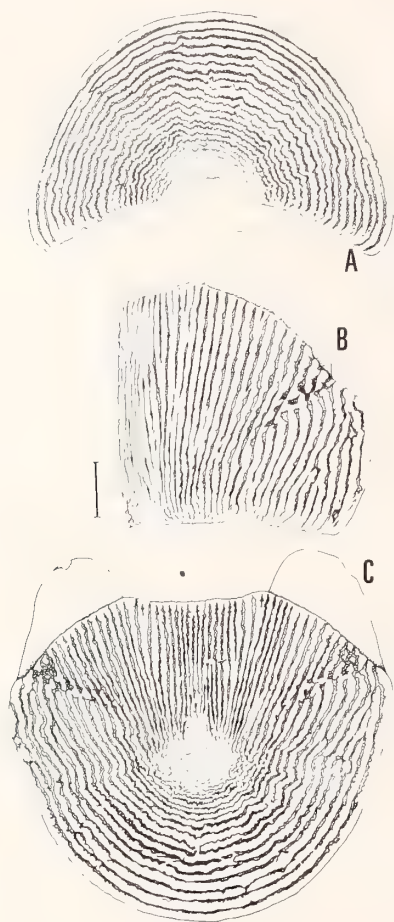


Figure 10

Stenoplax purpurascens (C. B. Adams). North side of Galeta Id., Panama (RCB). A, anterior valve. B, right portion of intermediate valve. C, posterior valve. Scale bar = 1 mm.

23 ribs per scale; ribs may or may not reach apex. Girdle fringe with straight, ribbed spicules approximately 97 μ m long.

Radula typical for subgenus. Denticle cap of major lateral tooth tricuspidate, moderately squat; small cusp pronounced; all cusps blunt; brown basal spot present.

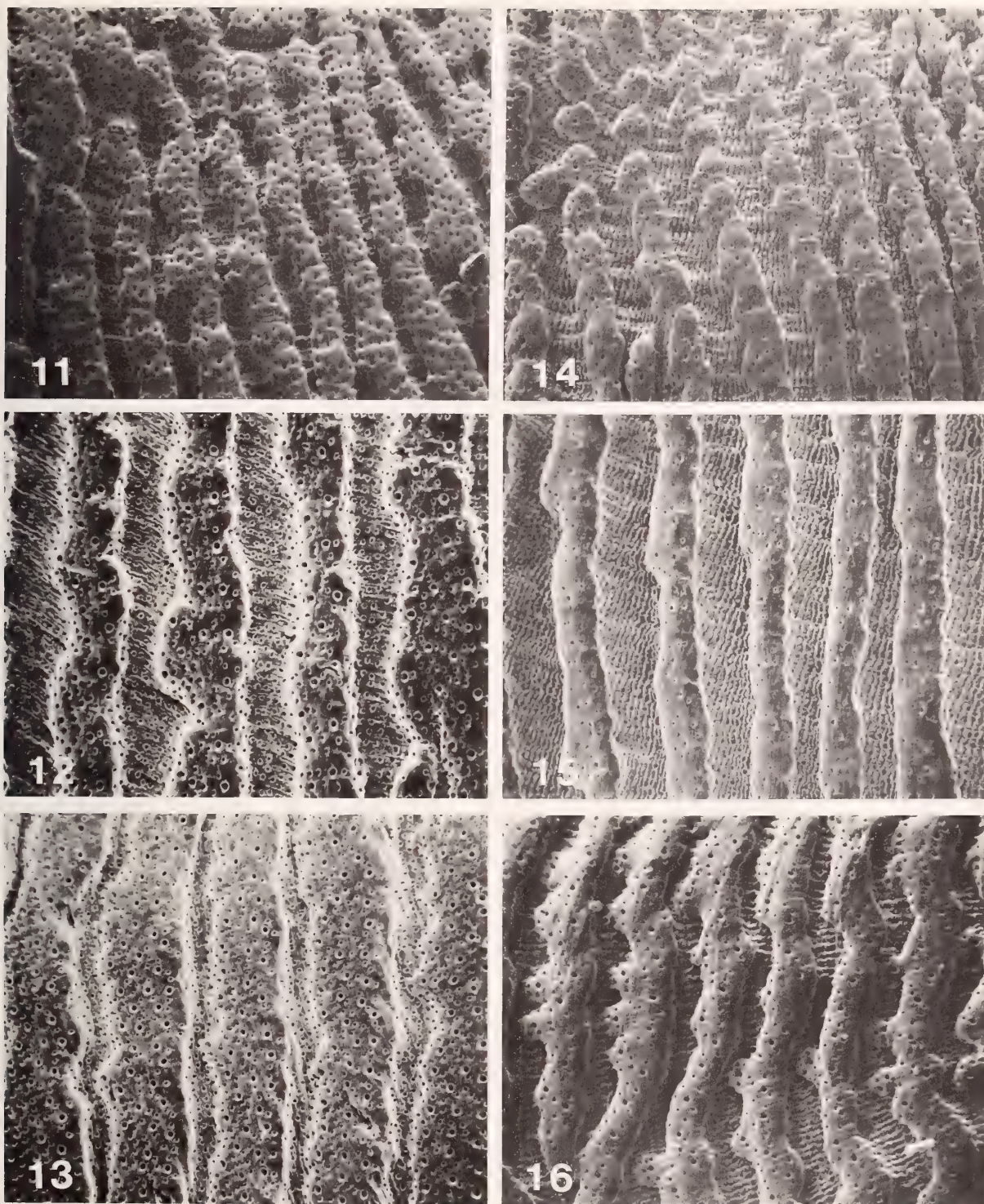
Remarks: There is much confusion in the literature about the relationship between the eastern Pacific *S. limaciformis* and the West Indian *S. purpurascens*. Sowerby's specimens were from Inner Lobos Island, Peru, and Guacomayo [southern Chiapas, Mexico, *vide* KEEN (1971)]. The general description given by Sowerby (*in* BRODERIP & SOWERBY, 1832) and the lack of specimens in museum collections certainly contributed to taxonomic chaos. DALL (1889) and PILSBRY (1892:57) both used Sowerby's name for the western Atlantic species that is herein recognized

as *S. purpurascens*. Pilsbry concluded that "the West Indian specimens collected by Robert Swift at St. Thomas and the Peruvian specimens which I have examined are absolutely identical in character . . ." THIELE (1909, 1910a) studied shell and girdle scale morphology of these species and he concluded that the West Indian species is not conspecific with *S. limaciformis*. Thiele's work, however, was ignored by American authors who continued to follow Pilsbry. ABBOTT (1954), KEEN (1958), and Thorpe (*in* KEEN, 1971), for example, all stated that *S. limaciformis* occurs in the Caribbean. KAAS (1972), who noted "rather striking differences between the two species," corroborated Thiele's earlier findings and he used the name *Ischnochiton purpurascens* (C. B. Adams) for the West Indian species. The culmination of this confusion is seen in ABBOTT's (1974) second edition of *American Seashells* in which he recorded both *S. limaciformis* and *S. purpurascens* from the western Atlantic.

FERREIRA (1978) was the first person to study large samples of New World *Stenoplax* from various localities. In his report on the status of the polyplacophoran species described from Jamaica by C. B. Adams, Ferreira examined the West Indian "*limaciformis*" problem in some detail. He concluded that differences in shell, girdle, and radular features do not warrant the use of the names *S. floridana* or *S. purpurascens*. FERREIRA (1978:88) found "many intergradations in the described tegmental sculptures, and many forms of transition between '*floridanus*' and '*limaciformis*' often in specimens found side by side at the same collection station." At the time Ferreira published his results, I was just beginning to examine *Stenoplax* specimens from Honduras and the Caribbean coast of Panama. I did not immediately see intergradations between *S. floridana* and *S. purpurascens*, and I therefore began a study that would allow me to decide independently the status of these *nomina*. My investigation began by using scanning electron microscopy to obtain high magnification photographs of the dorsal shell sculpture. Other parts of the investigation were devoted to an examination of the girdle elements and radulae using light microscopy.

I have concluded that *Stenoplax limaciformis*, *S. purpurascens*, and *S. floridana* are closely related but specifically distinct; furthermore, a third Caribbean species, *S. producta* (Reeve, 1847), exists. I can state that the reason that FERREIRA (1978) found differing entities "side by side at the same collecting station" is that each different western Atlantic species occurs sympatrically with another member of the group over a part of its range. Light microscopy of shell features, especially using glistening, alcohol-preserved specimens, can lead to confusion. But SEM studies of the shell and a study of denticle cap morphology have allowed the recognition of the subtle differences that characterize each member of this group of sibling species. Knowledge of these differences readily allows one to identify the species using a dissecting microscope.

Stenoplax purpurascens is more closely related to the eastern Pacific *S. limaciformis* than to *S. floridana* or *S.*



Explanation of Figures 11 to 16

Scanning electron micrographs of intermediate valve sculpture of *Stenoplax purpurascens* (C. B. Adams) and *S. producta* (Reeve). Posterior side toward top of page; all photographs 186 \times . Figures 11 to 13: *S. purpurascens*, Porto Bello, Panama (RCB). Figures 14 to 16: *S. producta*, Nassau, New Providence Id., Bahama Islands (GTW).

Figures 11, 14. Posterior region of central area near lateral triangle. Note the tendency for the ribs of *S. producta* to break into pustules near the lateral triangle, and the furrowlike sculpture in the intervening grooves.

Figures 12, 15. Central area near anterior margin. Note the low density of esthete pores on the ribs of *S. producta*.

Figures 13, 16. Lateral triangle.

Table 1

Esthete pore density and rib area measurements of members of the *Stenoplax limaciformis* species complex. All figures \pm SD. "Total" numbers derived from mean of each individual. See text for further explanations.

		\bar{x} SDEN/mm ²	\bar{x} LDEN/mm ²	\bar{x} TOTDEN/mm ²	\bar{x} PCTRA
<i>S. limaciformis</i> (n = 13)	TC	6348 \pm 1210	1388 \pm 299	7736 \pm 1369	59.4 \pm 6.6
	AM	5349 \pm 949	1248 \pm 162	6597 \pm 996	56.0 \pm 8.5
	LT	6383 \pm 1151	2086 \pm 305	8469 \pm 1306	68.8 \pm 6.2
	Total	6021 \pm 984	1611 \pm 223	7633 \pm 1123	61.5 \pm 6.1
<i>S. purpurascens</i> (n = 11)	TC	6798 \pm 1177	1278 \pm 128	8075 \pm 1222	68.9 \pm 7.1
	AM	5872 \pm 652	1166 \pm 157	7037 \pm 678	69.9 \pm 8.2
	LT	7505 \pm 1166	2089 \pm 422	9494 \pm 1286	75.5 \pm 5.9
	Total	6753 \pm 609	1524 \pm 166	8277 \pm 685	71.5 \pm 4.8
<i>S. floridana</i> (n = 11)	TC	4821 \pm 636	949 \pm 137	5770 \pm 752	47.9 \pm 7.6
	AM	2690 \pm 843	566 \pm 128	3257 \pm 898	43.5 \pm 6.4
	LT	5499 \pm 862	1119 \pm 239	6618 \pm 1051	54.8 \pm 4.3
	Total	4405 \pm 719	894 \pm 163	5300 \pm 832	48.6 \pm 4.4
<i>S. producta</i> (n = 6)	TC	3706 \pm 869	904 \pm 114	4610 \pm 962	56.4 \pm 3.4
	AM	2348 \pm 1144	512 \pm 118	2860 \pm 1260	56.6 \pm 7.4
	LT	5037 \pm 1215	1155 \pm 139	6192 \pm 1326	64.7 \pm 9.7
	Total	3790 \pm 1013	875 \pm 118	4665 \pm 1121	59.3 \pm 5.0

producta with which it occurs sympatrically over parts of its range. Both *S. purpurascens* and *S. limaciformis* have a centrally located mucro on the posterior valve and ribs on the central areas that do not form pustules near the lateral triangle. In addition, these ribs are broader and they have a much higher density of esthete pores than in *S. producta* and, especially, *S. floridana* (Table 1). The broadness of the ribs may be quantified by the area of the valve (as a percent) covered by ribs (PCTRA; see Table 1). All species except *S. floridana* have more than 50% of the intermediate valve covered by ribs; *S. purpurascens* has much higher values for PCTRA than the other species. Canonical variate analysis using the density of the megalopores (LDEN) and percent rib area (PCTRA) as variables reveals that two groups of the *S. limaciformis* species complex exist: one group is composed of *S. limaciformis* and *S. purpur-*

ascens while the other group consists of *S. floridana* and *S. producta*. The Mahalanobis D² distances, which reflect the distance between the centroids of each species, are much greater between these two groups than within each group (Table 2).

Both *Stenoplax limaciformis* and *S. purpurascens* have a brown basal spot on the denticle cap of the major lateral tooth. The denticle cap of *S. purpurascens* differs considerably by lacking the bulging outline along the side with the small cusp, and the small cusp is more prominent (Figures 8E, F). The species also differ in the sculpture of the lateral triangle, the anterior valve, and the posterior slope of the posterior valve. In *S. purpurascens* this sculpture typically is of rather flat, wavy, concentric ribs, whereas in *S. limaciformis* there is a much greater tendency for these ribs to be broken into broad nodules, especially on the end valves.

When compared with the other Caribbean species, *Stenoplax purpurascens* differs by its central, not posteriorly acentric, mucro on the posterior valve, and by wavy concentric ribs on the anterior valve. In both *S. floridana* and *S. producta* the anterior valve is granular, although some specimens of the latter species from 18 m at Gold Rock, Grand Bahama Island (FDNR 30416) interestingly differ in this respect and exhibit concentric sculpture. The lateral triangle of *S. producta* has concentric ribs, as does *S. purpurascens*, but the ribs in the former are typically more narrow, and they are parallel to the antero-posterior axis, rather than slightly oblique to it. The characteristic furrowlike sculpture in the grooves of *S. producta* (Figures 14–16), visible under high magnification in non-eroded specimens, serves to differentiate the species from

Table 2

Mahalanobis D² distance values between members of the *Stenoplax limaciformis* species complex. The distance values are in the upper triangle and probability values in the lower triangle. LIM = *S. limaciformis*, PUR = *S. purpurascens*, FLO = *S. floridana*, PRO = *S. producta*. See text for further explanations.

Species	LIM	PUR	FLO	PRO
LIM	—	1.94	5.89	4.61
PUR	<0.001	—	7.14	5.41
FLO	<0.001	<0.001	—	2.19
PRO	<0.001	<0.001	<0.05	—

S. purpurascens and other *Stenoplax* s.s. Both *S. floridana* and *S. producta* have a more elongate denticle cap on the major lateral tooth, the two larger cusps are more pronounced, and the brown basal spot, seen in *S. purpurascens*, is absent (Figures 8C, D, G, H).

FERREIRA (1978) mentioned that he had observed "many forms of transition" between members of the Caribbean *limaciformis* group. He did not state the localities where he had observed this phenomenon, but it is likely that he had encountered examples of either *Stenoplax producta*, which previous authors have not recognized, or some of the interesting intraspecific variation exhibited by *S. floridana*. *Stenoplax purpurascens* occurs sympatrically with *S. floridana* in the southern Caribbean (Panama and Colombia); it lives with *S. producta* in Cuba, Hispaniola, and Jamaica. In these cases I did not observe any intergradation; the shell sculpture indicated one species or the other, and these conclusions were consistently supported by SEM analysis of valve microsculpture and light microscopic observation of the radula.

Distribution: *Stenoplax purpurascens* occurs from Cuba and Hispaniola south and east through the Caribbean to Panama, the northern coast of South America, and Brazil (Figure 9A).

Specimens examined: *Cuba:* Gibara; Santiago (both GTW).—*Jamaica:* Montego Bay (MCZ); 2 mi (3.2 km) W of Runaway Bay, 1–1.5 m; along seawall, just W of Runaway Bay, 0.15–1 m (both RCB); Port Henderson (GTW).—*Haiti:* Miragoâne (MCZ).—*Dominican Republic:* Santa Bárbara de Samaná (MCZ); small cove just E of Embassy Beach, 16 km E of Boca Chica, 0.5–2 m; Isla La Matica, Playa Boca Chica, 0.5–1 m (both RCB).—*Puerto Rico:* Phosphorescent Bay; Magueyes Id., La Parguera; Cayo Enrique, La Parguera (all RCB); Arrecife Media Luna 2.25 mi (3.6 km) S of La Parguera (MCZ); Cabo Rojo Lighthouse (RCB); Playa Sucia, Cabo Rojo (MCZ).—*Virgin Islands:* Water Id., St. Thomas; St. Croix (both GTW); The Bight, Norman Id., 1–5 ft (0.3–1.5 m) (MCZ).—*Antigua:* Falmouth Harbour; Hawkes Bill Bay (both RCB).—*St. Lucia:* Vieux Fort (MCZ).—*Barbados:* Archers Bay, St. Lucy; Bridgetown (both RCB).—*Tobago:* (MCZ).—*Trinidad:* Maguaripe Beach, 1.5–3 m (RCB).—*Aruba:* Commanders Bay (RCB).—*Panama:* Toro Pt., ocean side (RCB); Galeta Id. (GTW, RCB); Reef off Cocal Pt., Porto Bello; Porto Bello (both RCB).—*Venezuela:* Cayo Punta Brava, Parque Nacional de Morrocoy, Tucacas (RCB).

Stenoplax floridana (Pilsbry, 1892)

(Figures 8G, H, 9B, 17–23)

Ischnochiton (Stenoplax) limaciformis (Sowerby). DALL, 1889: 415 [in part]. *Non Stenoplax limaciformis* (Sowerby).

Ischnochiton (Stenoplax) floridanus PILSBRY, 1892:58, pl. 17, figs. 19–22 (Key West, Florida; holotype ANSP 35694).

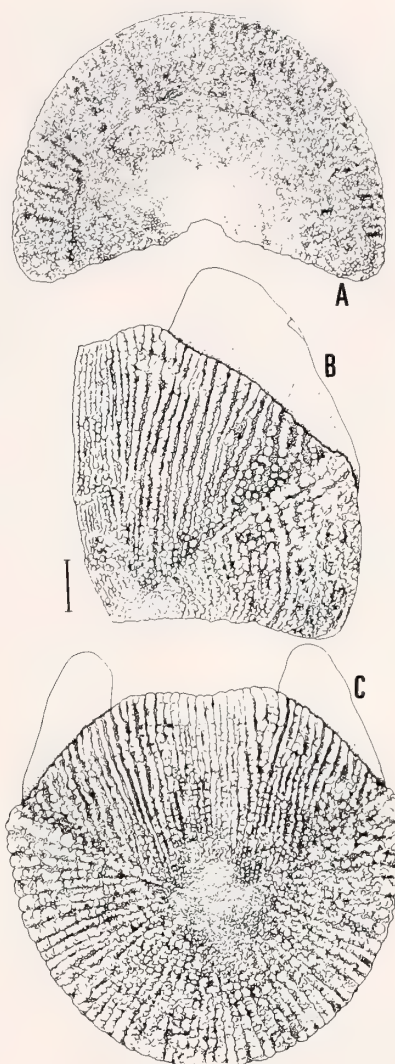


Figure 17

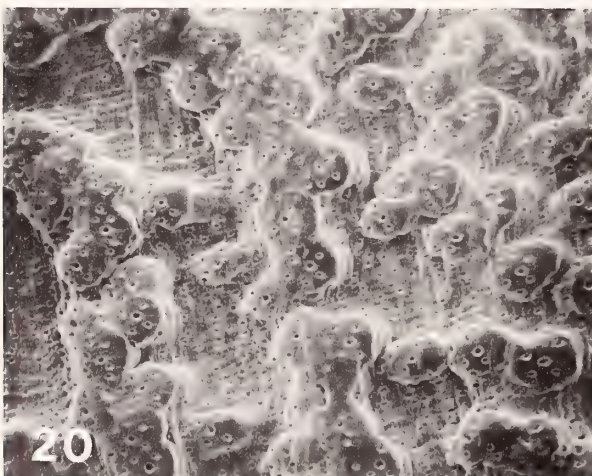
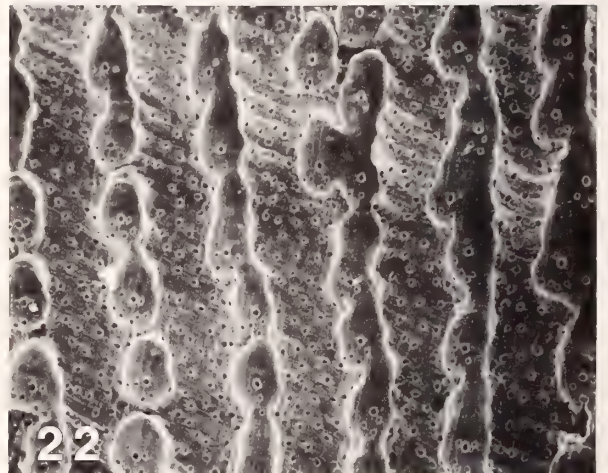
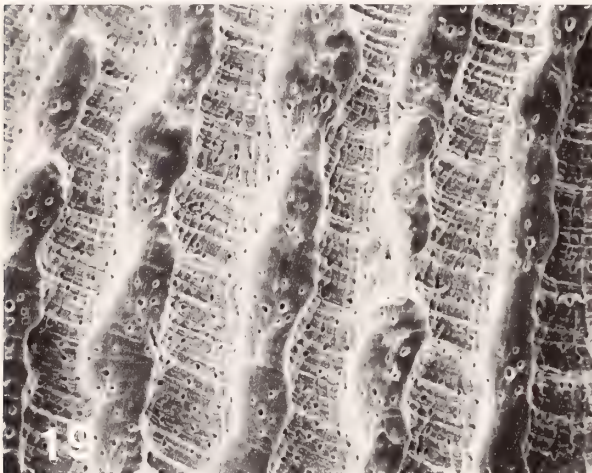
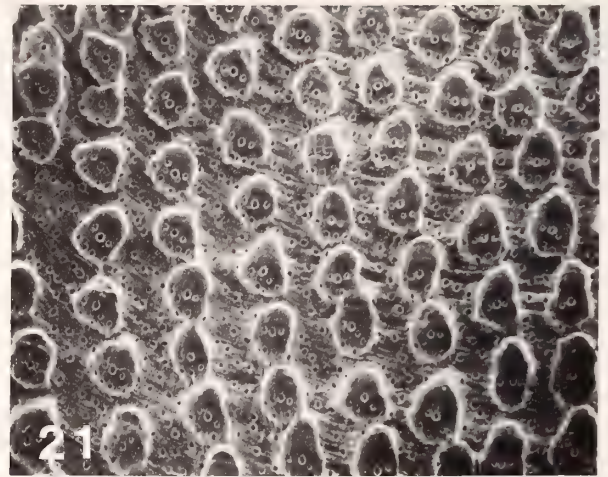
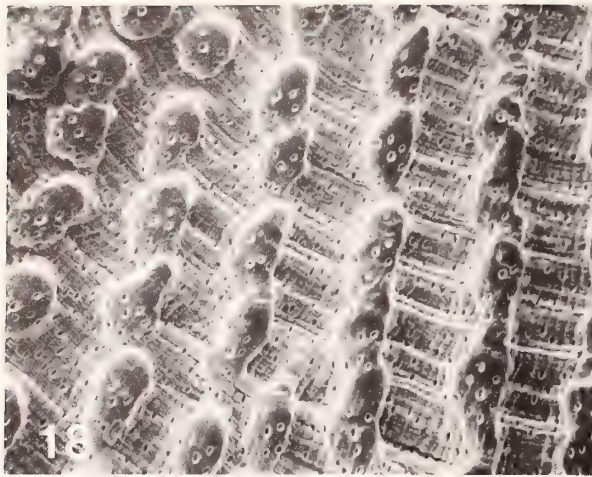
Stenoplax floridana (Pilsbry). Just north of Crawl Key, Florida Keys, Florida (RCB). A, anterior valve. B, right portion of intermediate valve. C, posterior valve. Scale bar = 1 mm.

Ischnochiton floridanus Pilsbry. JOHNSON, 1934:13; ABBOTT, 1954:320; GÖTTING, 1973:248, pl. 9, fig. 5.

Stenoplax floridana (Pilsbry). ABBOTT, 1974:396, fig. 4653; EMERSON & JACOBSON, 1976:464; TURGEON & LYONS, 1977:88; KAAS & VAN BELLE, 1980:48.

Stenoplax limaciformis (Sowerby). FERREIRA, 1978 [in part]: 87.

Description: Animal reaching a length of 50 mm, elongate. Color highly variable, but typically cream white with small dark green speckles. Anterior valve granular; small nodules may be radially or concentrically arranged, depending on growth lines; insertion plate with 8–11 slits. Intermediate valves moderately inflated, angular; longi-



Explanation of Figures 18 to 23

Scanning electron micrographs of intermediate valve sculpture of *Stenoplax floridana* (Pilsbry). Posterior side toward top of page; all photographs 186 \times . Figures 18 to 20: Indian Key Fill, Florida Keys, Florida (RCB). Figures 21 to 23: North side of Galeta Id., Panama (RCB).

Figures 18, 21. Posterior region of central area near lateral triangle. Note that the ribs are conspicuously broken into pustules, the sparseness of esthete pores on the ribs and pustules, and the lack of pronounced sculpture in the intervening grooves.

Figures 19, 22. Central area near lateral triangle.

Figures 20, 23. Lateral triangle.

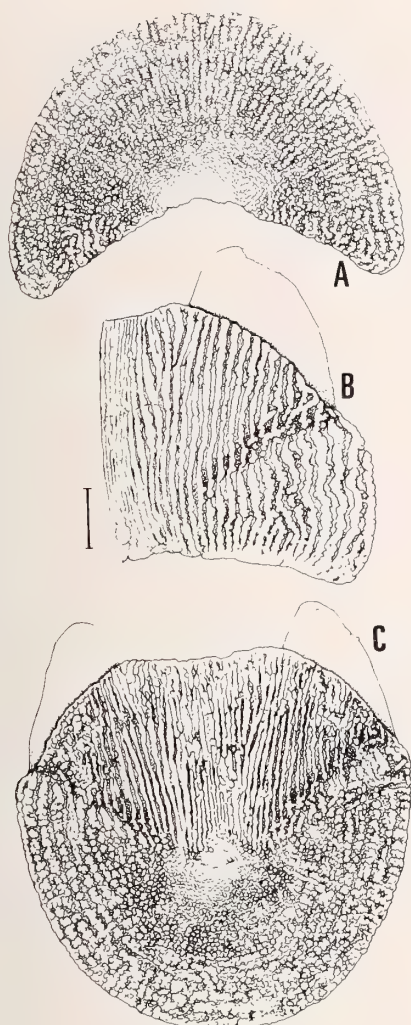


Figure 24

Stenoplax producta (Reeve). Arthur's Town, Cat Id., Bahama Islands (MCZ 279211). A, anterior valve. B, right side of intermediate valve. C, posterior valve. Scale bar = 1 mm.

tudinal ribs of jugum fine, directed anteriorly; ribs of central areas typically not as wide as intervening grooves, directed laterally; ribs broken into ovate to round pustules near lateral triangle; insertion plate with one slit per side. Lateral triangle sharply raised, with numerous small nodules which may be radially arranged or appear to be concentrically arranged due to heavy growth lines or slight coalescing of nodules. Posterior valve elongate; mucro posteriorly acentric; jugal area reduced; central area sculpture as in intermediate valves; posterior slope sculpture as in anterior valve; insertion plate with 8–12 slits.

Girdle scales about 100–125 μm long, 77–93 μm wide, 9–13 ribs per scale; ribs reach apex in some populations but conspicuously do not in other populations. Girdle fringe with straight, ribbed spicules 77–89 μm in length.

Radula typical for subgenus. Denticle cap of major lateral tooth tricuspidate, rather elongate; small cusp pronounced, all cusps pointed; outline of side with small cusp often quite straight occasionally inwardly curved; brown basal spot absent (Figures 8G, H).

Remarks: *Stenoplax floridana* is the most easily distinguished member of the *S. limaciformis* group. The consistent break-up of the longitudinal ribs of the central area near the lateral triangle into pustules allows instant recognition. The valve surface of *S. floridana* has much less surface area covered by ribs than the other species (Table 1). This reduction is due not only to the narrowness of the ribs but to the break-up of the ribs into pustules in the top central (TC) and lateral triangle (LT) areas. Although the ribs of *S. floridana* have a lower density of esthete pores than *S. limaciformis* or *S. purpurascens*, the density is higher than that observed in *S. producta*.

Long thought to be restricted to the Florida Keys, the species extends southward to the northern coast of Colombia (GÖTTING, 1973). *Stenoplax floridana* differs from *S. purpurascens*, with which it occurs sympatrically along the Caribbean coast of Panama and Colombia, by its more sharply raised lateral triangle which is granular, not with broad concentric ribs. Also, *S. purpurascens* never exhibits a break-up of the central area ribs into pustules. The denticle cap of the two species differs considerably: in *S. floridana* the denticle cap is more elongate, and an outline of the cap usually shows a straight side below the small cusp; the cusps of *S. floridana* are more pronounced and more pointed than those of *S. purpurascens* (Figures 8G, H). *Stenoplax floridana* lacks the brown basal spot of the denticle cap that is so characteristic of *S. purpurascens* and *S. limaciformis*. Some authors have noted that the girdle scales of the two species may be used as a differentiating character (PILSBRY, 1892; THIELE, 1910a; KAAS, 1972). There seems to be much intraspecific variation, often expressed on a geographic basis, in girdle scale morphology. Early in my investigation when I had sampled the scales of only a few individuals, I had also concluded that the girdle scales were taxonomically useful, but I now feel that statements concerning girdle scale differences must be made with caution. Scales of typical *S. floridana* from the Florida Keys have fewer ribs (9–12) than West Indian *S. purpurascens* (15–18); I never observed a rib count as low as that stated by KAAS (1972) who found 8 ribs. In the Florida Keys the ribs do not reach the apex, as Kaas noted, but this feature is certainly not true for populations of *S. floridana* from Honduras and Panama. Similarly, the girdle scales in some populations of *S. purpurascens* have ribs that do not reach the apex while other populations differ in this respect.

Stenoplax floridana is most likely to be confused with the previously overlooked *S. producta* (Reeve). Usually both species have a granular anterior valve and both often have thin ribs on the central areas; in *S. producta* these ribs occasionally show a slight break-up into pustules, but pustular formation is minimal. The lateral triangle of *S.*

producta has well developed concentric ribs whereas in *S. floridana* the lateral triangle is granular with the granules sometimes coalescing to form nodular radial ribs. In some specimens from Dry Tortugas and Key Largo, the granules partially coalesce to form irregular concentric ribs. Also, while some *S. floridana* have faint microscopic furrows in the intervening grooves, this feature is highly exaggerated in *S. producta*. The radular denticle cap of the two species differs considerably: in *S. floridana* the small cusp is pronounced and the remaining two cusps are elongated and pointed, whereas in *S. producta* the small cusp is often reduced and the other two cusps are broad and blunt (Figures 8C, D, G, H).

Distribution: *Stenoplax floridana* occurs from the offshore waters of the western coast of Florida to the Florida Keys and south to Honduras, Panama, and Colombia. The record from Nassau in the Bahama Islands has not been confirmed by recent collecting and it may be in error (Figure 9B).

Specimens examined: *Bahama Islands:* Nassau, New Providence Island (GTW).—*Florida:* Biscayne Bay (MCZ); Virginia Key; Old Spanish Light, Biscayne Bay (both GTW); Soldier Key (RCB); Ragged Keys (GTW, MCZ); Elliott Key (MCZ); Just E of Card Sound Bridge, Key Largo (RCB); Tavenier Key; Windley Key (both GTW); Tea Table Key; Indian Key Fill (both RCB); Indian Key (MCZ); Long Key, bay side (RCB); Conch Key; Grassy Key (both GTW); just N of Crawl Key (RCB); Crawl Key, bay side; Old Ferry Dock, Crawl Key; Bay Point, Crawl Key (all MCZ); Bonefish Key (GTW, MCZ); Pigeon Key (MCZ); Little Duck Key (GTW, RCB); Missouri Key (GTW, MCZ, RCB); Bahia Honda (GTW); West Summerland Key (RCB); Little Torch Key (MCZ); Pelican Shoals; Sambo Shoals (both GTW); Boca Chica (MCZ); Key West (GTW, MCZ); Long Key Reef, Dry Tortugas; N and E side of Bush Key, Dry Tortugas, 2–4 m; W side of Ft. Jefferson, Garden Key, 1–2 m; near moat wall, W side of Garden Key, Dry Tortugas, 0–2 m; SW corner of Garden Key, Dry Tortugas, 1.5–2 m; Bird Key Reef, Dry Tortugas, 0.5–1 m (all FDNR); BLM Sta. 151, 28°32'6"N, 084°18'54"W, 80–90 ft (24–27 m); BLM Sta. 047, 28°34'N, 084°20'12"W, 85–95 ft (26–28 m); BLM Sta. 251, 28°32'54"N, 084°6'24"W, 80–90 ft (24–27 m); BLM Sta. 247, 28°36'18"N, 084°9'42"W, 80–90 ft (24–27 m); BLM Sta. 146, 28°41'N, 084°23'18"W, 80–90 ft (24–27 m) (all approximately 110 mi [176 km] S of St. Marks, all DISL).—*Honduras:* Anthonys Key, Roatán Id. (RCB).—*Panama:* Galeta Id. (GTW, RCB); Verde Id., Mantilla Pt., Porto Bello (RCB).

Stenoplax producta (Reeve, 1847)

(Figures 8C, D, 9C, 14–16, 24)

Chiton productus REEVE, 1847:pl. 17, sp. 97 (Locality unknown [herein designated to be Eight Mile Rock, Grand Bahama Island]; holotype in BMNH).

Ischnochiton (Stenoplax) limaciformis (Sowerby). BOONE, 1933: 199, pl. 125, fig. A. *Non Stenoplax limaciformis* (Sowerby).

Stenoplax limaciformis (Sowerby). LYONS, 1981:38 (list). *Non Stenoplax limaciformis* (Sowerby).

Non Chiton productus 'Reeve' THIELE, 1909:7; 1910a:80; 1910b:110 [= *Stenoplax purpurascens* (C. B. Adams)].

Description: Animal reaching a length of about 30 mm, elongate. Color variable but usually speckled with green and white; slight rusty tinge often seen. Anterior valve usually granular; granules radially or concentrically arranged, depending on growth lines; insertion plate with 8–12 slits. Intermediate valves with fine longitudinal ribs on broad jugum; central areas with slightly flattened longitudinal ribs that are directed laterally; ribs almost as wide or wider than intervening grooves; ribs become irregular, but rarely break into a few pustules near lateral triangle; lateral triangle often sharply raised, with concentric ribs directed along antero-posterior axis; insertion plate with one slit per side. Grooves of lateral triangle and central areas with very fine furrowlike riblets visible at high magnification. Posterior valve elongate, mucro posteriorly acentric; jugal and central areas as in intermediate valves; posterior slope as in anterior valve, insertion plate with 8–11 slits.

Girdle scales about 118 μ m high, 76–97 μ m wide; 12–18 ribs per scale; ribs do not reach apex. Girdle fringe with straight, narrow spicules about 126 μ m long, 14 μ m wide.

Radula typical for subgenus. Denticle cap of major lateral tooth tricuspidate, rather elongate, small cusp somewhat reduced to nearly absent; two large cusps prominent, blunt; brown basal spot absent; elongate, V-shaped "tear" often present at base (Figures 8C, D).

Remarks: *Stenoplax producta* has remained unrecognized since its introduction by REEVE (1847). Although the locality of this species was unknown, most authors have listed the name in synonymy with *S. limaciformis* (Sowerby, 1832). After examination of the figures presented by Reeve, especially the "detail of sculpture" figure at the back of his work, and color and black-and-white photographs I made of the unique type specimen present in the British Museum (Natural History), I have concluded that Reeve's species is the Caribbean *Stenoplax* that one finds so commonly in the Bahama Islands. I herein designate Eight Mile Rock, Grand Bahama Island, as the type locality of *S. producta*. The type specimen exhibits concentric ribs on the lateral triangle that are directed along the longitudinal axis and not directed slightly obliquely as one sees in *S. purpurascens*, and the elongate posterior valve has a posteriorly acentric mucro. REEVE (1847: *Chiton* pl. 17, sp. 97) also seemed aware of the narrow ribs of his new species: he noted that the central areas were "longitudinally grooved" [stress on grooves]; in the next species listed, *Chiton sanguineus* [= *S. purpurascens*], he stated that the central areas were "very closely longitudinally striated" [stress on ribs]. All of these features lead one to recognize *S. producta* as the "Bahamian" *Stenoplax*.

REEVE's (1847) statements and illustrations do not completely agree with the British Museum specimen. Reeve clearly figures concentric ribs on the posterior slope of the posterior valve, and in the description he stated "terminal valves and lateral areas of the rest concentrically undulately striated." Although this statement is true for lateral triangle sculpture, the posterior slope of the single type specimen has a rather granular appearance due to a combination of radial and concentric arrangement of the granules. Whether Reeve for brevity's sake stressed "concentric," or whether the specimen Reeve described is no longer present in the type lot, is uncertain. Although *Stenoplax producta* typically has very granular areas on the anterior and posterior valves, it also can have wavy concentric ribs, as the specimens from Gold Rock, Grand Bahama Island attest (FDNR 30416).

There seems to be no doubt that *Stenoplax producta* is more closely related to *S. floridana* than to *S. limaciformis* or *S. purpurascens*. The denticle cap of the major lateral tooth of *S. producta* most closely resembles that of *S. floridana* and both types lack the brown basal spot observed on the denticle caps of *S. limaciformis* and *S. purpurascens* (Figure 8). Both *S. producta* and *S. floridana* have considerably fewer esthete pores, and a higher percentage of the valve surface is taken up by ribs, although in this respect *S. producta* is much more similar to *S. limaciformis* and *S. purpurascens* than to *S. floridana* (Table 1). Canonical variate analysis using the density of megalopores (LDEN) and percent rib area (PCTRA) indicates that *S. producta* forms a natural group with *S. floridana*; the Mahalanobis D^2 distance value is low when *S. producta* and *S. floridana* are compared, and high when *S. producta* is contrasted with the other two species (Table 2).

Distribution: *Stenoplax producta* ranges from the Bahama Islands and the offshore reef areas of the Florida Keys south to Cuba, Hispaniola, Jamaica, Honduras, and Isla de San Andrés (Figure 9C).

Specimens examined: *Florida:* Ragged Rocks (GTW); Looe Key (MCZ); Pelican Shoals (GTW); Sand Key, S of Key West, 0.5–2 m; Long Key Reef, Dry Tortugas; patch reef near Long Key Reef, Dry Tortugas, 1.5–2.5 m; N and E side of Bush Key, Dry Tortugas, 2–4 m; W side of Ft. Jefferson, Garden Key, Dry Tortugas, 1–2 m; SW corner of Garden Key, Dry Tortugas, 1.5–2 m; near moat wall, W side of Garden Key, Dry Tortugas, 0–2 m; Bird Key Reef, Dry Tortugas, 0.5–1 m; W side of Loggerhead Key, Dry Tortugas, 0–1 m (all FDNR).—*Bahama Islands:* *Grand Bahama Island:* Settlement Point, West End, 0–2 m; Sports Dock, West End, 0.5–1.5 m (both FDNR); shallow cove, 2 mi (3.2 km) W of Eight Mile Rock, 0–0.5 m; Eight Mile Rock, 1–2 m (both RCB); pool at entrance to underwater cave, E of Eight Mile Rock, 0.5–1 m (FDNR,RCB); W side of jetty, W of entrance to Freeport Harbour, 2–3 m (RCB); Jetty and adjacent bar, Caravel Beach, Freeport, 0–1.5 m; Gold Rock, 18 m; Deadman's Reef, 0.5–1.5 m; McLean's Town, East End, 1–2 m (all FDNR); *Bimini Islands:* Bimini

(GTW); North Lagoon, E coast of North Bimini (FMNH); Gun Cay, Bimini (MCZ); *Eleuthera Island:* Harbour Id. (GTW); Sand Pt., Savanna Sound (MCZ); *New Providence Island:* Nassau (GTW); Eastern Point; Fox Hill, South Beach (both MCZ); E of Clifton Pier, 1–2 m; Clifton Bluff, 4 m; Clifton Pt., 0–2 m (all RCB); *Cat Island:* Arthur's Town (MCZ); *Long Island:* Clarence Town (MCZ).—*Cuba:* Varadero (GTW).—*Jamaica:* 2 mi (3.2 km) W of Runaway Bay, 1–1.5 m; along seawall, just W of Runaway Bay, 0.5–1 m (both RCB).—*Haiti:* Gonâve Id.; Miragoâne (both MCZ).—*Dominican Republic:* Isla La Matica, Playa Boca Chica, 0.5–1 m (RCB).—*Isla de San Andrés:* Paradise Pt. (RCB).—*Honduras:* Anthonys Key, Roatán (RCB).

DISCUSSION

According to MAYR (1969:411), sibling species are "pairs or groups of closely related species which are reproductively isolated but morphologically identical or nearly so." The different species of the *Stenoplax limaciformis* complex are certainly very similar in appearance and the question that then remains is the determination of reproductive isolation. If the Caribbean species were geographically present as entirely allopatric groups of populations, which they are not, it might be convenient for some taxonomists, given the lack of major morphological differences, to assume that reproductive isolation had not been achieved and to view them as subspecies. But as WILEY (1981) noted, this approach, which is based on the view that species status has not been tested by sympatry, would lead to confusion. In the present paper it is shown that over part of its range each Caribbean species occurs sympatrically with another member of the group. *Stenoplax purpurascens* occurs with *S. producta* in Cuba, Hispaniola, and Jamaica; it is found with *S. floridana* in Panama and Colombia. *Stenoplax floridana* lives with *S. producta* on the offshore reefs of the Florida Keys and Roatán Island, Honduras. The fact that no hybrid zones are evident where sympatry occurs is conclusive proof that speciation has occurred. The allopatric *S. limaciformis* from the eastern Pacific must be considered specifically distinct from Caribbean members. It is as different from Caribbean members as the Caribbean members are from each other. It must be stressed that the small, but consistent, morphological differences observed among members of the *Stenoplax limaciformis* species complex strongly support the argument that species status has been achieved in each case.

The lack of biological information about *Stenoplax s.s.*, and chitons in general, prohibits any definitive statements about the restricted distribution of these species within the West Indian faunal province. The distributional pattern of members of the *S. limaciformis* complex in the West Indies, however, does suggest that their larvae remain planktonic for only a brief period. If this were not so one would expect broader distributional patterns within the West Indian province. The only report in the literature pertaining to the embryogeny of *Stenoplax* is that of HEATH

(1899) who reported that in *Stenoplax* (*Stenoradsia*) *heathiana* Berry, 1946, settlement of the larvae occurs during a period of 15 minutes to three hours after they become free swimming. A relatively short, but not as brief, planktonic existence is found in various other polyplacophorans (PEARSE, 1979). *Stenoplax purpurascens* occurs throughout the West Indies, yet it is conspicuously absent in the Bahama Islands and the Florida Keys. Its erroneously reported presence in Bermuda (CROZIER, 1920; ABBOTT, 1974) is based on specimens of *Stenoplax boogi* (Haddon, 1886). *Stenoplax floridana*, so abundant in the Florida Keys, is apparently lacking in the Bahama Islands, and *S. producta*, which is widely distributed in the western Caribbean, is commonly found at Dry Tortugas and offshore reefs of the Florida Keys, but not in the lower Florida Keys proper. It is likely that the Gulf Stream is a major disrupting force in the distribution of *Stenoplax*, not counting the fact that the distances involved, such as between Florida and the Bahama Islands, might be a sufficiently great barrier even if current patterns were more favorable.

Given the restricted distribution of *Stenoplax* s.s. within the West Indian faunal province, it would seem that the species might provide additional evidence for the theory of paraprovincialism as applied to the Caribbean (PETUCH, 1982). *Stenoplax floridana* and *S. producta* have a distributional pattern that reflects a Caloosahatchian origin, while the range of *S. purpurascens* indicates a Gatunian origin. The general current pattern in the Caribbean, which is from east to west, has probably kept *Stenoplax* species from extending their range eastward except for along continental margins; but even along continental shores large regions of mangrove and muddy substrates could prove to be an effective barrier. Thus, *S. floridana* and *S. producta* have probably been restricted to the western Caribbean and only *S. purpurascens* exists in the Lesser Antilles. *Stenoplax limaciformis* is the only species of the *S. limaciformis* group that is found in the eastern Pacific due to the continuous continental margin and the lack of insular environments. Shell and radular morphology of *S. limaciformis* are quite uniform throughout its extended range. It is lacking in offshore island groups, such as the Revillagigedo Archipelago (FERREIRA, 1983), Cocos Island (HERTLEIN, 1963), and the Galápagos Islands (SMITH & FERREIRA, 1977), which possess a fairly typical Panamic fauna.

Specific comments on the evolutionary relationships among the species of New World *Stenoplax* s.s. must await additional material. Adequate samples from the western Caribbean are especially lacking, but evidence available to date indicates that the *S. limaciformis* complex is composed of two distinct groups. The first group, whose members include *S. floridana* and *S. producta*, forms a lineage characterized by reduced rib width, fewer esthetes, and an elongate denticle cap. The second group, which includes *S. purpurascens* and *S. limaciformis*, has wide ribs, many esthete pores, and a rather squat denticle cap. These conclusions have been drawn from general observations of shell and radular morphology. The results of SEM anal-

ysis of valve microsculpture, especially the extent of rib surface area and the density of megalesthete pores, have provided corroborating evidence.

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A Comparison of Two Florida Populations of the Coquina Clam, *Donax variabilis* Say, 1822 (Bivalvia: Donacidae). II. Growth Rates

by

PAUL S. MIKKELSEN

Harbor Branch Foundation, Inc., R.R. 1, Box 196, Fort Pierce, Florida 33450

Abstract. Average summer growth rates of 3.0 mm and 3.7 mm per month were obtained for samples of *Donax variabilis* from southwest Florida and central eastern Florida, respectively, using length-frequency graphs. Individuals usually live only one year.

INTRODUCTION

PREVIOUS STUDIES ON the growth of *Donax variabilis*, the coquina clam, were done in Texas (LOESCH, 1957) and North Carolina (PEARSE *et al.*, 1942). However, these studies were conducted prior to the designation of a new species, *Donax dorotheae* Morrison, 1971, which occurs from northwest Florida to northeast Texas. In addition, many of the "young" of *D. variabilis* from the eastern United States now in the collections of the Smithsonian Institution and the Academy of Natural Sciences were determined to be *Donax parvula* Philippi, 1849 (see MORRISON, 1971), indicating identification problems in the past. MORRISON (1971) also split *D. variabilis* (as *D. roemeri* Philippi, 1849) into western (western Gulf of Mexico) and eastern (eastern Gulf of Mexico and eastern United States) subspecific forms. MARSH (1962) examined length-frequency graphs of *D. variabilis* collected during the summer and early fall from Pawleys Island, South Carolina, but found no well-defined size classes. Therefore, the growth rates of the eastern and western forms of *D. variabilis* possibly remain undetermined. In this paper, summer growth rates of *Donax variabilis* are given from two Florida populations, along with estimates of spawning periods and lifespan.

MATERIALS AND METHODS

Specimens of *Donax variabilis* were collected monthly (primarily for analysis of coloration and population density) from April through September 1976. Specimens were gathered from eight transects perpendicular to the beach, each consisting of about eight 15-cm diameter cores spaced at 1-m intervals within the intertidal zone of exposed sandy

beaches on the central eastern (Indialantic) and southwestern (Sanibel Island) coasts of Florida. Samples were sieved using a 1.2-mm mesh. The number of monthly cores varied due to the varying width of the swash zone being sampled at the time; the number of monthly cores averaged 40 at Sanibel and 49 at Indialantic Beach. Half of the transects were at 25-m intervals and half at 5-m intervals to decrease the possibility of missing localized aggregations of animals. *Donax parvula* was collected along with *D. variabilis* at the Indialantic site, but specimens of the former were separated and not analyzed for this study. Other information concerning sampling locations, methods, and times have been given previously (MIKKELSEN, 1981). Shell lengths were measured with calipers to ± 0.1 mm. The large samples of shells from Sanibel (excluding the April sample) were subsampled using a geological sediment sample splitter; all specimens from Indialantic were measured. Groupings to determine "sets" of individuals on length-frequency graphs were determined according to CASSIE (1954).

RESULTS

At Indialantic Beach, 477 specimens of *Donax variabilis* were collected and analyzed. One portion of the year class had somewhat regular monthly growth increments from May through August (crosshatched area, Figure 1). The mean shell length of these individuals increased from 7 mm in May to 18 mm in August, an increase of 11 mm over a period of 3 months, or an average summer growth rate of about 7.3 mm per month. Another set of young occurred, averaging 9 mm in length in the third week of September (stippled area, Figure 1).

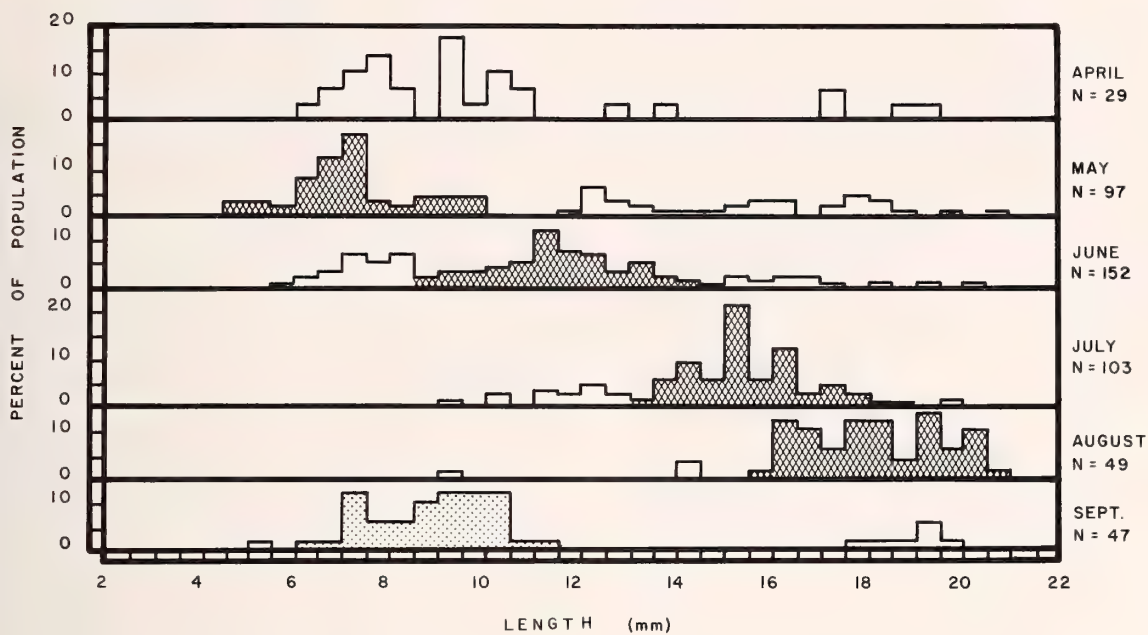


Figure 1

Length-frequency graphs of *Donax variabilis* from Indialantic (N = number of specimens). First set (crosshatched); second set (stippled).

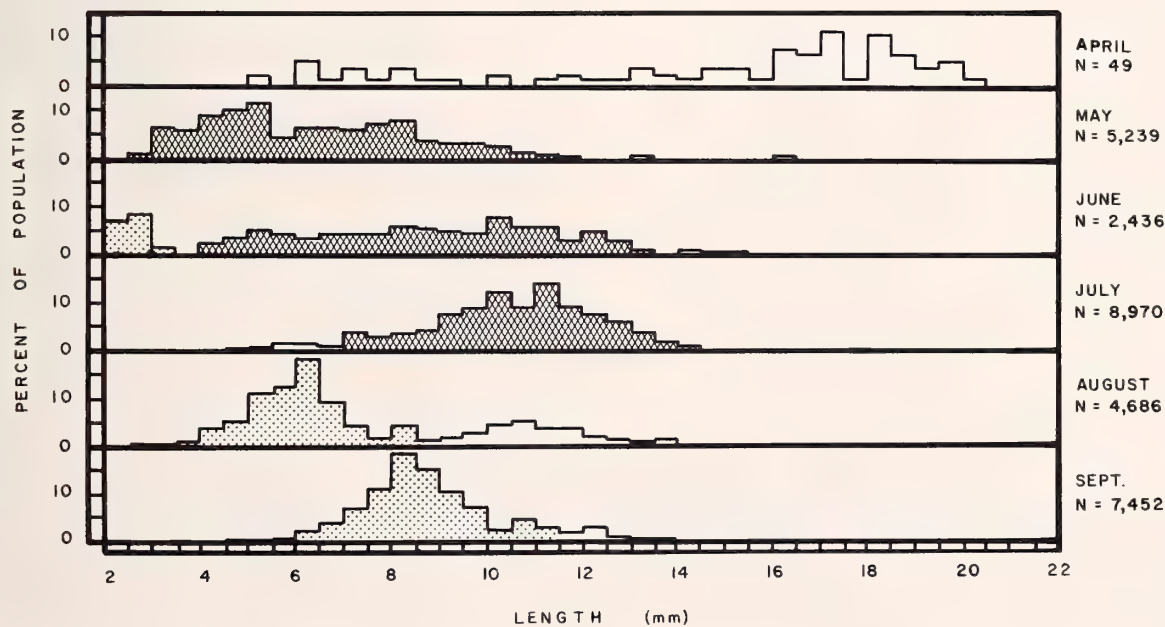


Figure 2

Length-frequency graphs of *Donax variabilis* from Sanibel (N = number of specimens). First set (crosshatched); second set (stippled).

At Sanibel, because 28,832 specimens were collected, subsamples provided manageable numbers, yielding monthly subsamples consisting of about 500 specimens each. The size classes could be followed from May through July (crosshatched area, Figure 2). The means of the distributions pass from 5 to 11 mm over a period of 2 months (May to July) and from 6 to 9 mm over 1 month (August to September), indicating an average summer growth rate of 3.0 mm per month. The Sanibel Island population also showed a second set of young (stippled area, Figure 2) around the first week of June; these had subsequently grown to a mean size of 6 mm by August and to 9 mm in September.

DISCUSSION

Constant movement of beach sands and contained clams, as well as the migratory ability of *Donax variabilis*, prevented use of a "mark-and-recapture" technique of growth measurement. Thus, repeated sampling of the population to construct length-frequency graphs was used, although problems exist with its use.

LOESCH (1957) in a study of two species of *Donax* pointed out that length-frequency curves can indicate growth only if (1) the mortality rate is the same for all sizes of individuals, (2) the clams enter the population as an entire group, and (3) there is no drift of specimens along the beach. In addition, permanent or temporary removal of individuals by wave action may wash specimens into the subtidal region (MIKKELSEN, 1981). Also, predators may selectively remove a particular size of clam. Many of the predators listed by LOESCH (1957) were confirmed during the present study, and to that list is added the Sheepshead fish, *Archosargus probatocephalus* (Walbaum, 1792); LEBER (1982a, b) added others. Selective removal by each of these predators seems likely and probably varied monthly depending upon the type, abundance, and size of the predators. This selectivity could have contributed to the skewing of the length-frequency data (Figures 1, 2), seemingly altering regular monthly growth increments present in individuals. Thus, growth alone may not be the reason for the position and rate of advancement of the modes and means present in the length-frequency graphs.

An additional factor is that the monitored population must consist of a single species. Approximately 54% of the *Donax* collected at Indialantic Beach were *D. parvula* and were not analyzed for this study. In his analysis of growth rate of *D. variabilis* from the Texas coast, LOESCH (1957) may have inadvertently included specimens of *D. dorotheae* and/or *D. texasiana*, similar but shorter and more obese species, whose ranges overlap that of *D. variabilis* in the western Gulf of Mexico. This factor could have influenced Loesch's lower growth rates of 1.75, 0.67 and 0.33 mm per month in his populations from three separate stations. However, this extreme variation may be real, and growth rates determined in the present study may be high because they are merely summer growth rates, rather than an

average over the year. Sanibel Island presented no identification difficulties because *D. variabilis* was the only donacid that occurred there.

Assuming a constant growth rate, the occurrence of numerous individuals in the May sample at Indialantic Beach whose lengths were clustered around 7 mm indicates a settlement approximately 7.5 weeks prior to that time, or about the first to second week of March. Thus, with a larval stage of 3 weeks average duration (CHANLEY, 1969), spawning may have been centered around the third week in February. The second group of young at Indialantic (averaging 9 mm in the third week of September) indicates a second spawning occurred on the east coast about 13 weeks earlier, or about the second week of June.

Following the same assumptions at Sanibel, settlement may have occurred, at 275 to 340 μ m (CHANLEY, 1969), around the second week of March, with spawning centered around the third week of February. This is essentially identical to the first spawning that occurred at Indialantic Beach. The second group of young at Sanibel indicated that a second spawning probably occurred about the second week of May and settlement about the first week of June. This second spawning at Sanibel was about 4 weeks earlier than the second spawning and settlement at Indialantic Beach.

Although spawning dates were extrapolated from length-frequency graphs, they may be reasonable estimates. Causes of error would include a more rapid growth rate for individuals younger than those examined. Correction for this error would yield spawning dates somewhat later in time. The dates reported herein differ, however, from those given for the North Carolina populations that were reported to have planktonic larvae from summer to fall (WILLIAMS & PORTER, 1971). LEBER (1982a) observed settlement of *Donax variabilis* in North Carolina during February and November.

The general absence of an abundance of large *Donax variabilis* throughout the summer months indicates that most of those specimens that had matured the previous fall and winter had probably died, although some may have moved and remained offshore. This suggests that the majority of individuals probably live for approximately 1 year, with a few entering a second year. This is consistent with the findings of LOESCH (1957) and PEARSE *et al.* (1942) who also used length-frequency graphs. MARSH (1962) also noted fall declines in the intertidal density of *D. variabilis*. Although LEBER (1982a, b) attributed fall declines in the number of *Donax variabilis* to emigration to subtidal levels, LEBER (1982a, fig. 3) also noted only a few large specimens entering a second year (at least intertidally). However, MORRISON (1971), who compiled data by measuring museum specimens, determined a 2-yr life span.

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Comparative Shell Microstructure of North American *Corbicula* (Bivalvia: Sphaeriacea)

by

ROBERT S. PREZANT AND ANTONIETO TAN-TIU

Department of Biological Sciences, University of Southern Mississippi,
Hattiesburg, Mississippi 39406

Abstract. Comparative microstructural analyses of the shells of the North American "purple" and "white" forms of *Corbicula* reveal no significant differences. Shells of both forms are composed of an outer crossed-lamellar and an inner complex crossed-lamellar microstructure. Adductor myostracum in *Corbicula* is reported for the first time. The wide variation in internal shell coloration is not reflected in shell microstructure. Internal growth bands, of possible daily origin, have been found within the crossed-lamellar region of the valves.

INTRODUCTION

THE PROLIFIC NATURE of the exotic bivalve *Corbicula* sp. in North America, and its incidental fouling characteristics, has stimulated considerable efforts to understand the biology of this organism. Most previous research has assumed that a single species of *Corbicula* (*C. fluminea*) resides in North America. Recently, however, HILLIS & PATTON (1982) presented evidence that two species of *Corbicula* are found sympatrically in at least some Texas river systems. These authors based their suggestion on electrophoretic data (allelic differences at 6 of 26 genetic loci) and on morphometric data including internal shell color, shell shape, and number of shell annuli. Although the electrophoretic data are difficult to discount (and indeed are supported by additional fixed loci discovered by McLEOD [1984]), HILLIS & PATTON (1982) concede that "differences in number of annuli may reflect differences in microhabitat preferences for the two forms." In the Brazos River, Texas (locations of Hillis and Patton's *Corbicula* populations), microhabitat distinctions may include differences in water flow and siltation rates. HILLIS & PATTON (1982) typically found a form of *Corbicula* with predominantly white internal shell coloration ("white" forms) in less energetic areas with higher siltation rates, and forms with predominantly purple internal shell coloration ("purple" forms) in rocky areas with faster moving waters. PREZANT & CHALERMWAT (1984), by modifying the clam's environment in the laboratory, have found that "white" forms with purple highlights may be induced toward totally white internal shell coloration. It was also found by the latter authors (1983) that clams maintained

at warm temperatures under specific high organic conditions, as well as unhealthy or moribund animals, produced an internal crossed acicular microstructural pattern. This type of microstructure is significantly different from the typical complex crossed-lamellar pattern found in non-stressed or healthy clams of the same population. It was suggested that this modified shell type reflected stressful conditions, with animals devoting their energies toward life sustaining functions and away from normal shell production.

The taxonomic uncertainty that presently exists in North American corbiculid systematics, in conjunction with possible ecophenotypic shell modifications produced in the laboratory, prompted this comparative study of shell microstructure of the two forms of North American *Corbicula*. Scanning electron microscopic studies revealed no significant microstructural differences between shells of the two color forms but has revealed an adductor myostracum and some interesting observations on corbiculid shell formation. In addition, very subtle differences (not statistically significant in our populations with our methodology) in total organic content were noted in the two forms.

MATERIALS AND METHODS

Shells of both the "purple" and "white" forms of North American *Corbicula* were obtained from collections made in December 1981 from the San Gabriel River, Williamson County, Texas, U.S.A., by Dr. D. Hillis. Live "white" forms were collected from Tallahala Creek, Perry County, Mississippi, U.S.A. in July 1983. Soft tissues were removed from the Tallahala Creek specimens and all shells

were dehydrated in absolute ethanol for five days, followed by critical point drying in a Denton DCP-1 Critical Point Drier using liquid carbon dioxide as a transfer agent. Some specimens were free fractured prior to critical point drying. Specimens were mounted on aluminum stubs using silver paint, coated with a thin layer of gold in a Polaron SEM Coating Unit E5100, and examined on an AMR 1000A scanning electron microscope at accelerating voltages of 30 kv. At least four specimens from each group were examined.

Organic content of shell of each form (*i.e.*, Texas "white" and "purple") was determined by combustion of crushed valves in groups of four (run in triplicate) or individually (seven valves of each) for 2 h at 550°C. PALMER (1983) determined that 2 h provided optimum time for combustion of organics in shell material without significant conversion of CaCO_3 to CaO . Valves were weighed to the nearest 0.05 mg and significance tested by Student's *t*-test (two-tailed) at 2% significance level.

All figures, except Figure 1, are scanning electron micrographs.

RESULTS

Internal Coloration

The two forms, according to HILLIS & PATTON (1982), differ in several morphometric features including overall proportions (ratio of length, height, thickness) and number of shell annuli. These differences, however, are often difficult to discern (COUNTS, 1983). Of particular interest is the difference in internal shell pigmentation. According to HILLIS & PATTON (1982) the more elongated clams (greater length/height ratio) with greater number of annuli tend to possess an internal shell with a deep purple pigmentation. We have found a great deal of variation in intensity of color as well as extent of coverage. The interior of some valves is entirely purple while others have a lighter coloration over some or all the valve interior (Figure 1). In particular, the hinge teeth retain a lighter pigmentation. The full range of pigmentation in the "purple" forms runs the gamut from complete coverage of light or dark pigmentation; deeply colored only dorsal to the pallial line; deeply colored only ventral to the pallial line; deep purple highlights only beneath the umbone; or strong pigmentation only posterior to the posterior adductor scar.

Forms with stouter (lower length/height ratio) shells and fewer annuli show a lighter ("white") internal shell coloration usually with only a light purple tinge (Figure 1). Frequently, however, deeper purple coloration is found ventral to the pallial line. Specimens of "white" forms collected from Tallahala Creek, Mississippi, usually show deeper purple highlights than "white" forms collected in Texas. Larger Tallahala Creek specimens often exhibited alternating concentric bands of white and purple on the shell interior.

Specimens collected dead (*i.e.*, empty valves) are char-

acterized by a dull chalky internal shell coloration as opposed to the lustrous finish in living, healthy animals. Animals that die in the lab often have a lustrous, white internal shell coloration. Differences in these various shell forms are described elsewhere (PREZANT & CHALERMWAT, 1983, 1984).

Shell Microstructure

There were no significant differences in shell microstructure between "purple" and "white" forms from San Gabriel River, Texas, and the "white" forms from Tallahala Creek, Mississippi. All specimens possess a bilayered aragonitic shell composed of an internal complex crossed-lamellar and an outer crossed-lamellar microstructure. An evident pallial line indicates the transition zone between these two microstructures.

At high magnifications the interior surface of both shell forms ventral to the pallial line appears finely granular (Figure 2). This reflects the internal surface features of laths composing the crossed-lamellar region. In fracture section the bidirectional nature of the laths in this region is quite clear (Figure 3). Laths of this region in both color forms approximate 0.16 μm in thickness. A regular series of fine growth bands is particularly evident in radial fractures through the crossed-lamellar region near the valve edge (Figure 4) in "purple" specimens collected in December in the San Gabriel River, Texas. These bands average 9.4 μm in width with about 106 bands per mm near the periphery of a 25-mm long clam.

The inner shell layer of both forms is conical complex crossed-lamellar in microstructure (Figures 5, 6) (terminology from CARTER, 1980). Laths of this structure in both forms average 0.2 μm thick. The surficial, internal junction between complex crossed-lamellar and crossed-lamellar regions occurs in the form of a gradual transition zone over the pallial line (Figure 7). On the internal surface this zone occurs as a progression of emerging complex crossed-lamellar polygonal lath tips over smooth pallial myostracal surface (Figures 7 to 9). Lath tips range in width from 2.5 to 3.8 μm in both forms. The irregularity of direction of these tips reflects the tridirectionality of internal lamels. In fracture sections the division between the complex crossed-lamellar layer and the crossed-lamellar layer is demarcated by a zone of small prisms that often leads directly to the complex crossed-lamellar pattern externally but may also grade into a blocky zone that then leads to the complex crossed-lamellar region (Figure 10).

The surficial tips of the complex crossed-lamellar laths often decrease in size close to the umbones in "white" forms (Figure 11). Umbonal area laths are also less regular in their polygonal tip shapes. Their smoother, finer surfaces may be a result of erosion.

Infrequently, the complex crossed-lamellar surface in "purple" forms near the pallial line forms a different surficial pattern for this type of microstructure. In these cases



Figure 1

Variation in internal shell color (reflected in black, white, and shades of gray) of North American *Corbicula*. The two columns on left represent the "white" forms and those in the right columns the "purple" forms. All specimens collected from San Gabriel River, Texas, by D. Hillis.

the laths protrude farther from the plane of the shell, are less angular near their tips, and are much smaller in width (Figure 12). These laths average less than $0.5\ \mu\text{m}$ in width and are extremely crowded. An apparent organic deposit is often found covering small portions of this type of surface microstructure in "purple" forms (Figure 13). This organic film forms a smooth, contoured layer filling in and "flowing" over each irregularity of this surface, and may reflect an active growth zone.

Adductor Scars

Internal surfaces of both the anterior and posterior adductor scars of the white and purple forms show concen-

tric lines (Figure 14), which appear "lighter" than the surrounding area when viewed with the scanning electron microscope. In all samples, a transition zone was observed along the peripheral region of the adductor scars nearer the umbone. The relatively smooth internal surfaces of the muscle scars merge with the irregular emerging lenses of the first order lamellae of the complex crossed-lamella (Figure 15). This marks the region where the adductor scars are being grown over by complex crossed-lamellae. This is analogous to the event occurring at the pallial line. The opposing peripheral half of the adductor scars, on the other hand, did not show distinct boundaries with the outer crossed-lamellar layer.

Radial fractures through adductor scars of both white

Explanation of Figures 2 to 10

Figure 2. Internal surface view of crossed-lamellar microstructure ventral to the pallial line near valve edge. San Gabriel white form. Horizontal field width = $14\ \mu\text{m}$.

Figure 3. Fracture section through crossed-lamellar zone. Purple form. Horizontal field width = $13\ \mu\text{m}$.

Figure 4. Radial fracture through crossed-lamellar region near valve edge showing periodic growth bands. Direction of growth is to the left. Purple form. P, periostracum. Horizontal field width = $940\ \mu\text{m}$.

Figure 5. Radial fracture showing cone complex crossed-lamellae. Very top of micrograph shows internal surface of this region. Merger into crossed-lamellae is revealed near bottom of micrograph. Purple form. Horizontal field width = $67\ \mu\text{m}$.

Figure 6. Radial fracture of cone complex crossed-lamellar zone. Purple form. Horizontal field width = $14\ \mu\text{m}$.

Figure 7. Surficial view of the junction between complex crossed-lamellar (K) and crossed-lamellar (L) regions at the pallial line (B). Tallahala white form. Horizontal field width = $74\ \mu\text{m}$.

Figure 8. Lath surface tips of complex crossed-lamellar microstructure. Shell edge toward top of micrograph. Tallahala white form. Horizontal field width = $32\ \mu\text{m}$.

Figure 9. Complex crossed-lamellar lath tips. Shell edge toward top of micrograph. Purple form. Horizontal field width = $16\ \mu\text{m}$.

Figure 10. Fracture section showing merger between complex crossed-lamellar (K) and crossed-lamellar (L) regions. Note blocky merger laths. Purple form. Horizontal field width = $27\ \mu\text{m}$.

Explanation of Figures 11 to 19

Figure 11. Modified complex crossed-lamellar surface near umbone. San Gabriel white form. Horizontal field width = $16\ \mu\text{m}$.

Figure 12. Complex crossed-lamellar surface just dorsal to the pallial line. Purple form. Horizontal field width = $15\ \mu\text{m}$.

Figure 13. Organic deposit (O) covering surface of complex crossed-lamellar region just dorsal to the pallial line. Purple form. Horizontal field width = $8\ \mu\text{m}$.

Figure 14. Internal surface of posterior adductor scar. Tallahala white. Horizontal field width = $3.4\ \text{mm}$.

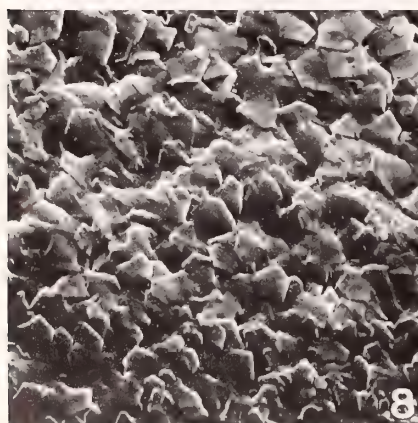
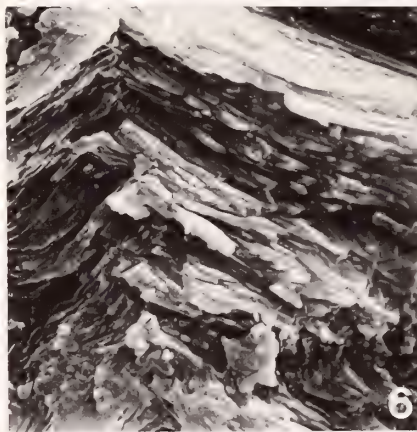
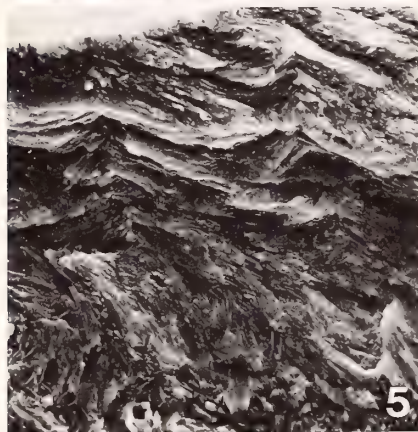
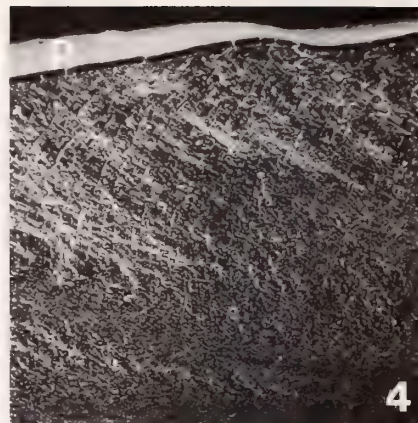
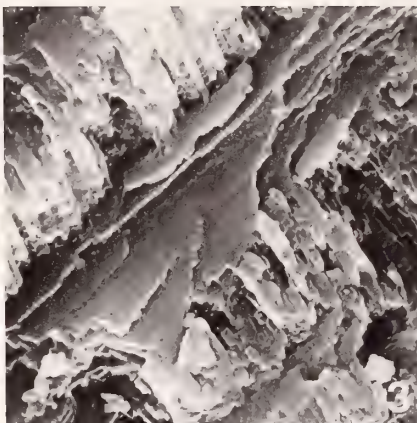
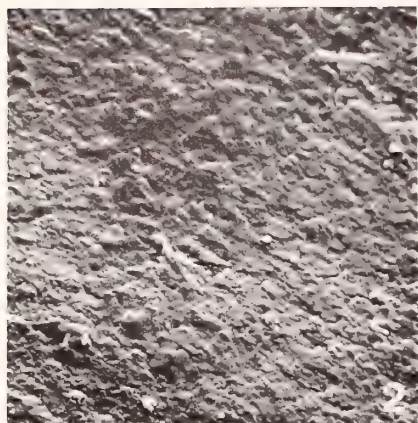
Figure 15. Internal surface of transition zone between complex crossed-lamella (K) and myostracum (A) of posterior adductor scar. Purple form. Horizontal field width = $80\ \mu\text{m}$.

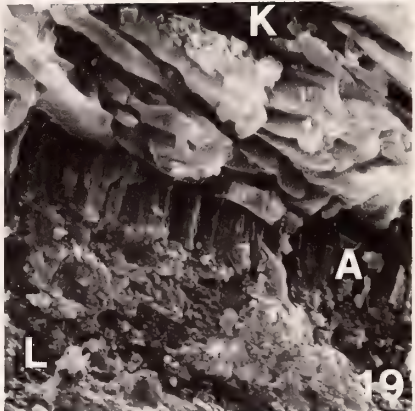
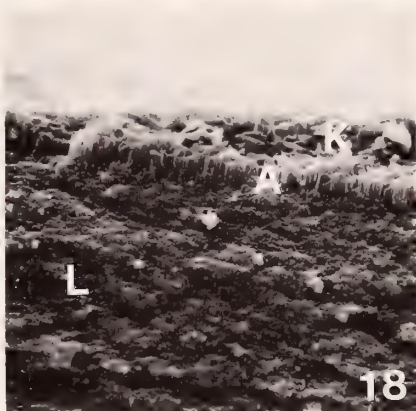
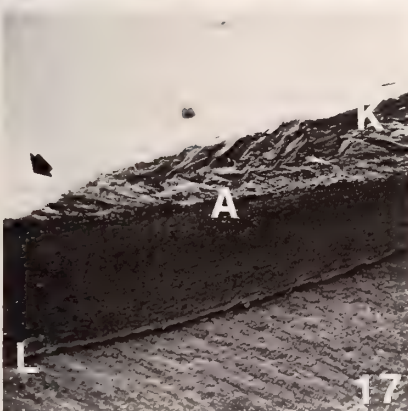
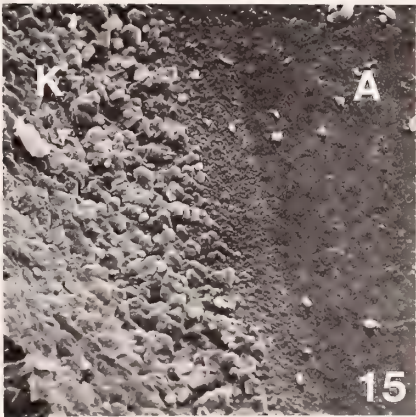
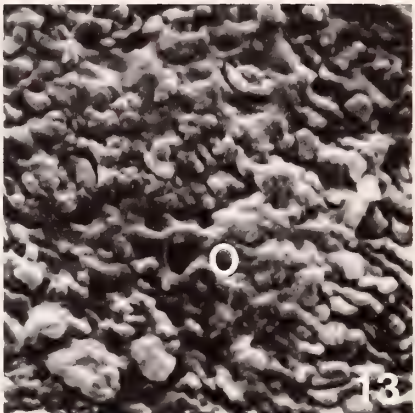
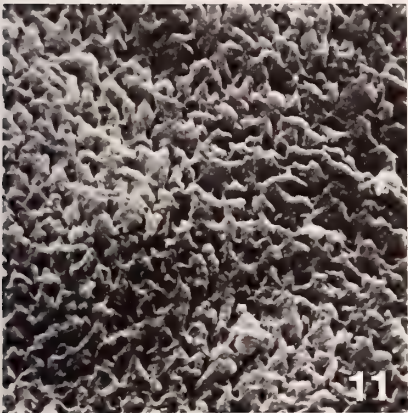
Figure 16. Radial fracture through anterior adductor scar. Myostracum (A), crossed-lamella (L). Purple form. Horizontal field width = $16\ \mu\text{m}$.

Figure 17. Radial fracture through portion of anterior adductor scar (arrow) and complex crossed-lamella (K), submerged myostracum (A), crossed-lamella (L). Dark line (at L) represents internal fracture between lamellae of the crossed-lamellar layer oriented in opposing directions. Purple form. Horizontal field width = $415\ \mu\text{m}$.

Figure 18. Radial fracture dorsal to posterior adductor scar. Part of complex crossed-lamella (K), myostracum (A), crossed-lamella (L). Tallahala white form. Horizontal field width = $33\ \mu\text{m}$.

Figure 19. Radial fracture dorsal to anterior adductor scar. Complex crossed-lamella (K), myostracum (A), crossed-lamella (L). Purple form. Horizontal field width = $13\ \mu\text{m}$.





and purple forms revealed a thin internal surface prismatic layer, about $1.7\ \mu\text{m}$ high (Figure 16), composing the adductor scars. Submerged myostracal prisms are embedded between the internal complex crossed-lamella and the outer crossed-lamella extending from the transition zones toward the umbones (Figures 17 to 19).

Shell Organics

Results of organic combustions of individual valves varied between 1.06 to 6.62% and between 2.32 and 2.70% for bulk determinations. Purple forms averaged slightly more overall organic shell content than white forms, but both methods (*i.e.*, bulk and individual valve determinations) yield averages that are not significantly different at the 2.0% level using a Student's *t*-test. For bulk determinations, the white valves averaged ($\bar{x} \pm 1\ \text{SD}$) $2.45\% \pm 0.05$ shell organics and the purple valves $2.50\% \pm 0.19$. Individual valve determinations showed an average for the white form of $2.49\% \pm 1.07$ and $3.30\% \pm 1.87$ for purple forms.

DISCUSSION

While some morphometric and biochemical differences between "purple" and "white" forms of North American *Corbicula* may be significant taxonomic features to indicate separation of the two forms into species (HILLIS & PATTON, 1982; MCLEOD, 1984) (although COUNTS [1983] showed statistically significant overlaps between purple and white forms based on shell morphometry), shell microstructure cannot be added to the list. MACKIE (1978) suggests that "habitat type and temperature do not affect the type of crystals formed in sphaeriacean shells and that crystal type is under genetic control." The microstructural shell differences between the two forms examined here are subtle and likely reflect individual variations. These variations may reflect growth stages, erosive patterns, or modified microenvironments. The present research has revealed, however, some important features of *Corbicula* shell microstructure (*i.e.*, growth bands, adductor myostracum, *etc.*) and stimulates some interesting questions concerning biomineralization.

CARTER (1979) suggested that crossed-lamellar shell structures might yield important "signatures" for addressing taxonomic and phylogenetic problems among extant and fossil bivalve mollusks. PREZANT & CHALERMWAT (1983) have shown, however, that some complex crossed-lamellar microstructures are plastic and may be "shaped" by basic physiologic conditions. There is great import in this microstructural shell flexibility and great care must be taken when using these shell features in approaching taxonomic problems in mollusks.

Differences in organic content between the two forms determined with the methods used here are not statistically significant at the 2% level using a Student's *t*-test. Although the reported differences in shell organics be-

tween white and purple forms from Texas show no statistical significance, this does not necessarily preclude the potential biological importance reflected in the slightly higher average organic content of purple valves. "White" forms showed slightly less overall shell organic content than "purple" forms; this might reflect microhabitat differences. "Purple" forms, found in faster moving waters (HILLIS & PATTON, 1982), may produce a thicker periostracum, or the organic difference may reflect an organic nature of the purple pigmentation. Further studies are needed to elucidate the significance of any organic differences.

Of interest to biomineralogists are the gradual transitions noted between the two major microstructural forms found in *Corbicula* shell. The growth of complex crossed-lamellar laths apparently proceeds with small "nuclei" being deposited as incipient laths. These are gradually added to and form the final polygonally tipped, elongate laths. Directed growth toward a central focus outside the plane of the shell accounts for the conical nature of this structure.

To our knowledge there have been no reports of internal shell growth lines in *Corbicula* prior to this study. LUTZ & RHOADS (1977) and GORDON & CARRIKER (1978) have clearly shown the relationship between growth lines in bivalves and subdaily shifts in pH, and shell dissolution. The high regularity of growth bands in *Corbicula* may indicate a process of active calcareous shell deposition alternating with growth stoppage. There is no evidence of irregular internal shell banding patterns that would indicate an active seasonal period of shell production disrupted by irregular periods of shell dissolution in the Texas population examined. We are presently investigating the possibility that the growth increments are of a daily nature.

Adductor myostracum was not observed in *Corbicula* "*fluminea*" from Japan, *C. occidentalis* Deshayes from India, *Corbicula* sp. from Lake Nyanza (TAYLOR *et al.*, 1973) nor *C. fluminea* examined by MACKIE (1978). However, this shell layer was consistently present in samples we examined. Furthermore, there are no significant differences in microstructure of adductor scars between "white" and "purple" forms of *Corbicula*.

The arrangement of growth lines on the adductor scars suggests that the anterior adductor is migrating anteroventrally, while the posterior adductor is migrating posteroventrally as they grow. The mantle on the leading edge of the adductor is responsible for the formation of the myostracum whereas the mantle on the trailing edge produces the covering complex crossed-lamella. Adductor scar growth lines suggest localized areas rich in organic material.

The phenomenal spread of *Corbicula* in North America (McMAHON, 1982) is sound testimony to the general adaptiveness of this bivalve. The lack of distinguishing microstructural features between the two North American

forms of *Corbicula* may be indicative of plesiomorphic characters that are well established, successful, and unaltered within the family. This concurs with the basic microstructural shell trends found at the superfamily level by KENNEDY *et al.* (1969). The similarities, on the other hand, may reflect a taxonomic basis for retaining a single species for the two forms. The total evolutionary and taxonomic status of North American Corbiculidae is yet to be completely discerned.

ACKNOWLEDGMENTS

Many of the corbiculid valves used in this study were graciously supplied by Dr. David M. Hillis. The manuscript has been improved by the constructive comments of Dr. R. McMahon, Mr. K. Chalermwat, and three anonymous reviewers. Many thanks also to Ms. E. Henderson for typing the manuscript and Ms. S. DuBois for dark-room assistance.

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A New Species of *Sphenia* (Bivalvia: Myidae) from the Gulf of Maine

by

ROBERT W. HANKS¹

National Marine Fisheries Service, North Atlantic Coastal Fisheries Research Center,
Laboratory for Ecology and Pathology of Marine Organisms, Oxford, Maryland 21654

AND

DAVID B. PACKER²

Marine Systems Laboratory, National Museum of Natural History, Rm. W-310,
Smithsonian Institution, Washington, D.C. 20560

Abstract. A new species of the genus *Sphenia* Turton, 1822, is described from the Gulf of Maine. Also, a lectotype for *Sphenia binghami* Turton, 1822, type species for the genus, is designated. *Sphenia sincera* Hanks & Packer, spec. nov., is easily distinguished from other members of the genus. It is the first *Sphenia* reported from the northeast coast of the United States, and, unlike other *Sphenia*, *S. sincera* is not found in a nestling habitat. The unique, undistorted shell of *S. sincera* reflects this habitat difference. The new species remained undetected until now because it had been confused with juveniles of the well-known *Mya arenaria* and *M. truncata*. *Sphenia sincera* differs from species of *Mya* in the shape of the chondrophore, small adult size, short life span, and completely subtidal occurrence. The species is found in greatest abundance at depths from 30 to 63 m. Unlike species of *Mya*, *S. sincera* prefers soft silt-clay sediments where it may be a deposit-feeder as well as a filter-feeder. It appears to be a major food item for bottom-feeding fish.

INTRODUCTION

THE GENUS *Sphenia* Turton, 1822, is one of the lesser known taxa in the bivalve family Myidae. Small size, nestling habit, and rarity in collections have restricted scientific interest in the group to taxonomic and faunistic studies. On the other hand, the genus *Mya* Linné, 1758, owing to commercial importance, wide distribution, and great abundance, has been studied intensively. Species of *Mya* are found on parts of all coastlines of the Northern Hemisphere; species of *Sphenia* have been reported from the Atlantic and Pacific coasts of North and South America, from Japan and Korea, from Puerto Rico, from the

Atlantic coast of Europe, and from the Mediterranean Sea (HABE, 1951; WARMKE & ABBOTT, 1961; KEEN, 1971; ODE, 1971; RIOS, 1975; ROSEWATER, 1975; TEBBLE, 1976; BERNARD, 1983). Some *Sphenia* are said to occur on the South African, Indian, and Malay coasts (LAMY, 1919), but documentation is poor. *Sphenia binghami* Turton, 1822, the type species of the genus by subsequent designation of GRAY (1847), has been recorded along the shores of the Eastern Atlantic from Morocco north to the British Isles and into the Mediterranean (TEBBLE, 1976).

Several specimens of *Sphenia* were dredged from the Sheepscot River estuary in 1956, during studies of the benthic fauna of the midcoast region in the Gulf of Maine (HANKS, 1961, 1964). In subsequent years, large numbers of this small bivalve were collected from deep waters of the estuary, from coastal regions, and from fish stomachs. *Mya arenaria* Linné, 1758, is abundant in this region, and *M. truncata* Linné, 1758, has been reported. Although the

¹ Current address: National Marine Fisheries Service, New England Liaison Office, P.O. Box 425 DTS, Portland, Maine 04112.

² Reprint requests should be sent to this author.

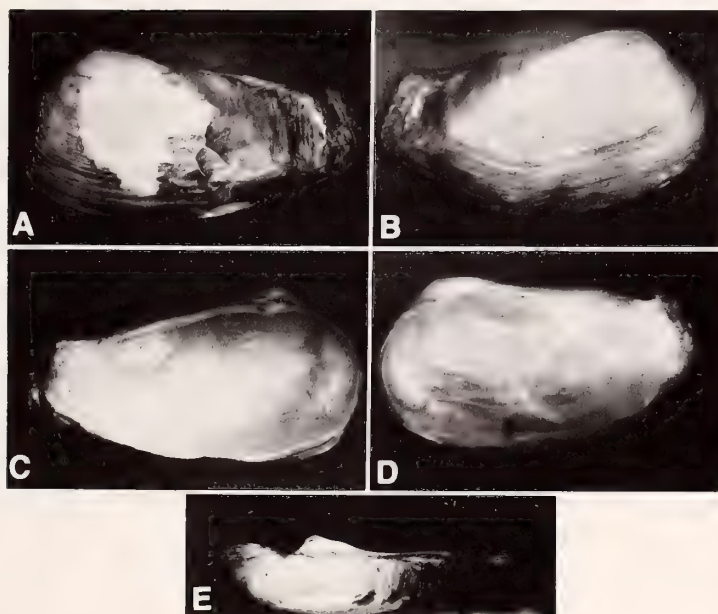


Figure 1

Lectotype herein of *Sphenia binghami* Turton, 1822, USNM 171240. $\times 4.7$. A and B, outer surface of left and right valves. C & D, inner surface of left and right valves. E, chondrophore of left valve.

two species of *Mya* are easily separated as adults, juvenile *Mya* and any stage of *Sphenia* might easily be confused. Great abundance and a few previously unidentified museum specimens indicate that this new species of *Sphenia* has long been an inhabitant of the Maine coast, but it has remained unknown because of its small size and similarity to *Mya*, in combination with a habitat entirely different from that of other *Sphenia*. The presence of a new species of *Sphenia* in the northwestern Atlantic represents a significant addition to the known range of the genus.

Family MYIDAE Lamarck, 1809

Subfamily Spheniinae Bernard, 1983

Sphenia Turton, 1822

Type species: *Sphenia binghami* TURTON, 1822:36, pl. III, figs. 4, 5; by subsequent designation GRAY, 1847:190.

To the best of our knowledge, no type specimen has previously been identified. Turton's original material appears to have passed to the Jeffreys collection and thence into the U.S. National Museum of Natural History, where specimens labeled "*Mya binghami* Turton, ex. mus. Turton. Jeffreys Coll. #75" (USNM 171240) were found. The allocation to *Mya* can be ascribed to Jeffreys, who did not feel that Turton was justified in erecting a new genus (JEFFREYS, 1862-1869:vol. 3, p. 72). The specimens found were two, separated but matched, pairs of valves, one unseparated pair, several unmatched right valves, and

what appears to be a piece of old oyster shell bored by *Cliona* in which are several minute *Sphenia*. Although none of these specimens matches TURTON's (1822) figure, it is believed that this material was part of his original collection. Therefore, one of the matched pairs (remaining in USNM 171240) that was most similar to that of Turton's original description is here designated as lectotype (Figures 1, 2). The remainder of this material is designated as paralectotypes (USNM 679166). The designation of the lectotype parallels the action of DAVIS (1964) in identifying type specimens of other Turton species, where there is sufficient evidence that the original material is now in the U.S. National Museum of Natural History.

TURTON's original description (1822) was brief and somewhat ambiguous, and it led to descriptive errors by later authors. For example, Turton said (p. 36), "From the *Mya* it [*Sphenia*] differs, in having the valve which contains the tooth smaller, and received within the opposite one; in being closed at the hinder extremity; and in being furnished with a concave tooth in the larger valve, behind which is a small denticle." In reality, the left valve in both *Mya* and *Sphenia* is the smaller and bears the relatively large chondrophore. NICOL (1958) commented on this point as follows: "A few of the related Myidae are also inequivalve, having in all such cases larger right than left valves." In young *Mya* and undistorted *Sphenia* the posterior end is closed and the two valves fit tightly together. Also, the concavity in the right valve occurs in both genera.

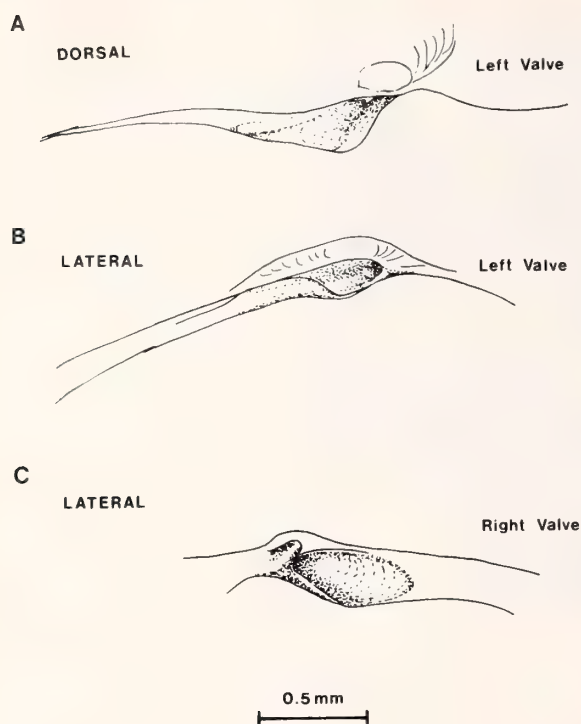


Figure 2

Hinge structure of *Sphenia binghami* Turton, 1822, lectotype USNM 171240. A, dorsal view of chondrophore of left valve. B, lateral view of chondrophore of left valve. C, lateral view of resilifer of right valve.

Turton's description of the species *Sphenia binghami* was, fortunately, accurate. FISCHER (1887) and LAMY (1919) correctly described the *Sphenia* hinge.

Although *Sphenia binghami* is the best known species of the genus, most accounts deal superficially with the shell morphology, and only two descriptions of the entire animal have been published (FORBES & HANLEY, 1853; YONGE, 1951); the latter description is by far the more complete. Accounts of other species of *Sphenia* consist primarily of records of new species or distributions, and emphasize shell morphology (e.g., CARPENTER, 1864; SMITH, 1893; DALL & SIMPSON, 1901; etc.).

Sphenia sincera Hanks & Packer, spec. nov.

(Figures 3–5)

Description—External: Shell elongate; strongly inequivalve, right valve larger and more deeply cupped. Posterior gape small; siphons completely withdrawable into shell. Umbones prominent, often eroded; one-third the length from anterior end; prosogyrate; umbo of right valve larger than left. Anterior end inflated, generally rounded;

dorsal margin somewhat straighter than ventral, sloping gradually and evenly to posterior end, which may be slightly rounded or vertical. Color chalky white; rarely with a narrow, dark orange-brown color along margins. Thin, yellowish periostracum sometimes present, but generally eroded from valves, covering only paired siphons. Surface with fine, irregular concentric growth lines. A distinct ridge running from umbo to posteroventral angle, more acute on left valve.

Internal: Shell smooth, dull white. Adductor scars and pallial line usually obscure. Anterior scar long; tear shaped; extending to, or slightly past horizontal midline of shell. Posterior scar oval; higher than wide (width two-thirds of height); one-half distance between umbo and posterior. Pallial line well back from edge of shell and complete between anterior and posterior adductor scars, joining ventral margin of pallial sinus in an acute angle at a point directly below posterior adductor scar. Pallial sinus small, "U" shaped; extending anteriorly two-thirds distance between posterior and umbo; dorsal margin attached to adductor scar at a slight angle.

Hinge: Nomenclature for the myid hinge follows BERNARD (1979a) based on FUJIE (1957) and MACNEIL (1965) (Figure 4).

Left valve: Chondrophore narrow, strongly arched, resulting in ligamental pit being directed in an oblique anterior angle. Ligamental pit small; anterior ridge prominent, its junction with ventral or outer margin directly opposite or posterior to umbo. Radial groove large as a consequence of posterior ridge being directed in an oblique posterior angle. Posterior ridge expanded and flattened, not projecting sharply beyond outer margin; median groove shallow and open, often represented by a median undulation. Anterior buttress vestigial; posterior buttress much reduced laterally, generally extended posteriorly. Deep pit under umbo for tooth of right valve.

Right valve: Resilifer concave, ovate-trigonal, dominated by a projecting blunt tooth on anterior end that articulates with anterior surface of anterior ridge in left valve. Lateral end of tooth fitting into concavity under umbo of left valve, as in a ball and socket joint, possibly providing movement about dorsoventral axis (see TRUEMAN, 1954).

Type locality: Mouth of the Sheepscot River, Lincoln County, Maine (69°42'W, 43°47'N); depth 33.6 m; soft mud, primarily silt and clay. Full description of associated fauna and environment can be found in HANKS (1964) and LARSEN (1979).

Holotype: U.S. National Museum of Natural History, USNM 679164.

Dimensions of the holotype: Length 5.6 mm, height 4.0 mm, width 2.5 mm, umbo to anterior 2.2 mm, umbo to posterior 3.4 mm, chondrophore length 1.43 mm, chondrophore width 0.34 mm.

Paratypes: USNM 679165. The balance of our collection remains in our possession at the National Marine Fish-

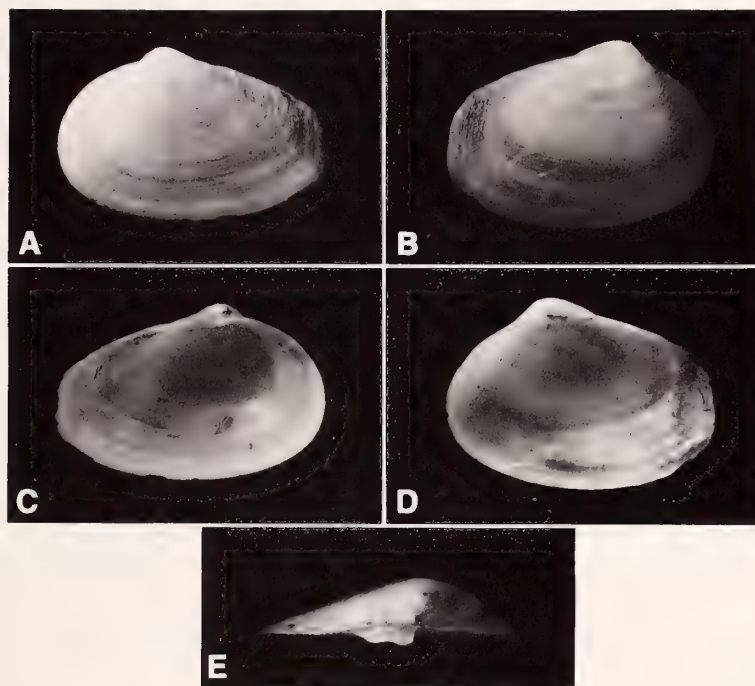


Figure 3

Holotype of *Sphenia sincera* Hanks & Packer, spec. nov., USNM 679164. $\times 6.3$. A and B, outer surface of left and right valves. C and D, inner surface of left and right valves. E, chondrophore of left valve.

eries Service, Oxford, Maryland 21654, and the Marine Systems Laboratory of the Smithsonian Institution in Washington, D.C. 20560. In addition, the following is a list of previously unidentified material in the U.S. National Museum of Natural History now assigned to *Sphenia sincera*: 1 specimen from Casco Bay (Portland), Maine, USNM 150763; 6 specimens from off Mt. Desert Island, Maine, 16.5 m, USNM 173122; 7 specimens from Bar Harbor (Mt. Desert Island), Maine, USNM 199189; 1 specimen from off Gotts Island (Mt. Desert region), Maine, USNM 451224; 2 specimens from off Gotts Island, Maine, USNM 451230; 75+ specimens from Frenchman Bay, Maine, USNM 451334; 1 specimen from Winter Harbor (Mt. Desert region), Maine, USNM 451368; 4 specimens from Frenchman Bay, Maine, USNM 462652.

Total number of specimens collected was about 977, of which about 350 have been closely examined. The average length of 70 *Sphenia sincera* shells, collected in June of 1962, was 5.4 mm, with a range of 3.4 to 8.9 mm. The average height of these shells was 3.6 mm, with a range of 2.4 to 5.3 mm. The largest shell collected from the Sheepscot region was 9.9 mm in length.

Etymology: The specific epithet *sincera*, derived from the Latin *sincerus*, which is defined as "clean, natural, without

mutilation," refers to the undistorted shape of the valves, a feature rarely found in the genus *Sphenia*, as well as to their clean, brilliant whiteness.

Distribution: Known populations of *Sphenia sincera* are centered around the mid-coast region of Maine, near Boothbay Harbor and the mouth of the Sheepscot River in the south and Gouldsboro Bay in the north. It is likely that *S. sincera* has a continuous distribution from about Casco Bay in the south (sandy sediments become prominent farther southward), to perhaps the coast of Nova Scotia in the North (Figure 6).

Comparisons: Nearly all previous records, with the exception of those for *Sphenia antillensis* Dall & Simpson, 1901 (DALL & SIMPSON, 1901; WARMKE & ABBOTT, 1961; RIOS, 1975), have reported species of *Sphenia* to be nestlers living in the burrows constructed by other invertebrates. On the coast of England, *S. binghami* is frequently found living in the vacant burrows of *Hiatella* (YONGE, 1951). Every account of European *S. binghami* emphasizes the shell distortion caused by conformity to crevices and burrows formed by other animals (FORBES & HANLEY, 1853; JEFFREYS, 1865; TEBBLE, 1976; see also BALUK & RADWAŃSKI, 1979, for a comparison of *S. binghami* with its presumed Neogene ancestor, *Sphenia anatina* Basterot,

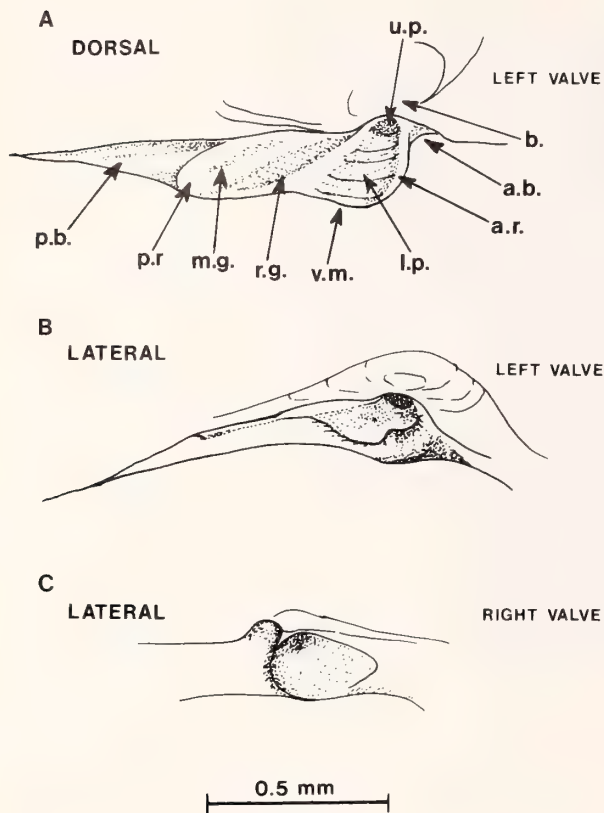


Figure 4

Hinge structure of *Sphenia sincera* Hanks & Packer, spec. nov., holotype USNM 679164. A, dorsal view of chondrophore of left valve. B, lateral view of chondrophore of left valve. C, lateral view of resiliifer of right valve. Key: b, beak or umbo; u.p., umbonal pit; a.b., anterior buttress; a.r., anterior ridge; l.p., ligamental pit; v.m., ventral or outer margin; r.g., radial groove; m.g., median groove; p.r., posterior ridge; p.b., posterior buttress.

1825). Generally, the shell posterior is truncate or rostrate and is usually distorted by the confines of its habitat (STANLEY, 1970; BALUK & RADWAŃSKI, 1979). Often, the posterior region of the shell is weakly calcified, which gives flexibility to the shell, and apparently this feature has selective value for the nestling species. Additionally, YONGE (1951) stated that lack of mobility and the nature of the habitat is further indicated by the presence of encrusting growths on the shell and periostracum of the siphons.

In contrast, *Sphenia sincera* has none of the characteristics of the typical nestling form, and has not been observed in a nestling habit, although *Hiatella* is common on the rocky New England coastline (THEROUX & WIGLEY, 1983), and extensive collections were made throughout the lower Sheepscot estuary in the dense *Hiatella* populations adjacent to deep-water populations of *S.*

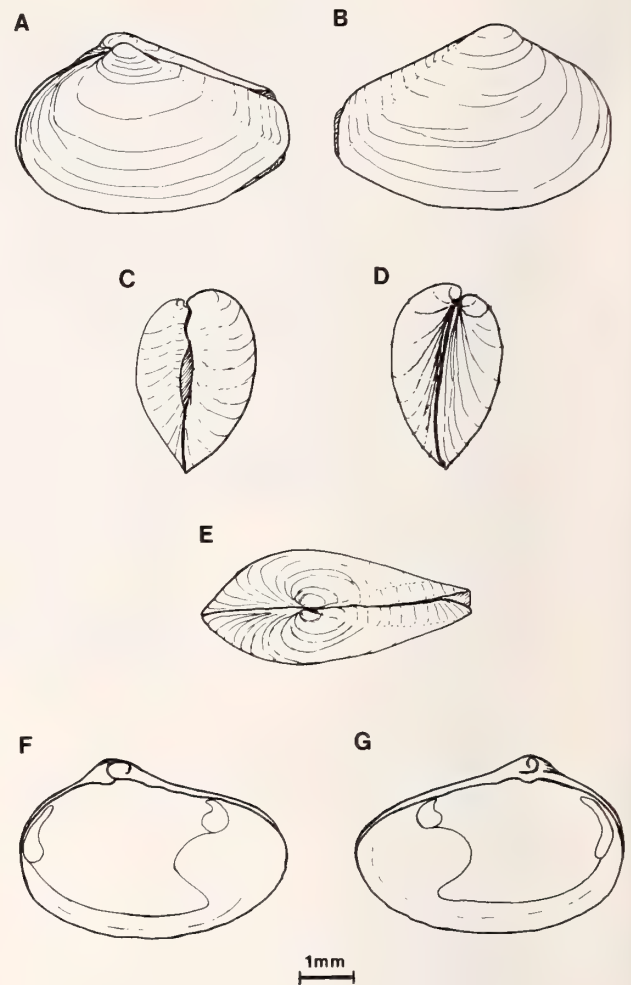


Figure 5

Sphenia sincera Hanks & Packer, spec. nov. Camera lucida drawing of holotype USNM 679164. A, left valve. B, right valve. C, posterior. D, anterior. E, dorsal view. F, inner surface of right valve. G, inner surface of left valve. Pallial complex usually obscure, but has been highlighted in this drawing.

sincera. The burrows and tubes of other organisms were also examined closely. *Sphenia sincera* is always found living on or near the surface of the soft, clay-silt mud found along the Maine coast. The shells are never distorted, and the periostracum is quite thin. In most respects they resemble the juveniles of *Mya arenaria* and *Mya truncata*, but *S. sincera* differs from *Mya* in having a chondrophore that is more strongly arched, a reduced ligamental pit, an expanded radial groove, and an anterior ridge that joins with the outer margin directly opposite or posterior to the umbo (never anterior as in *Mya*). Also, the pallial sinus is shallower and does not extend to the middle of the shell.

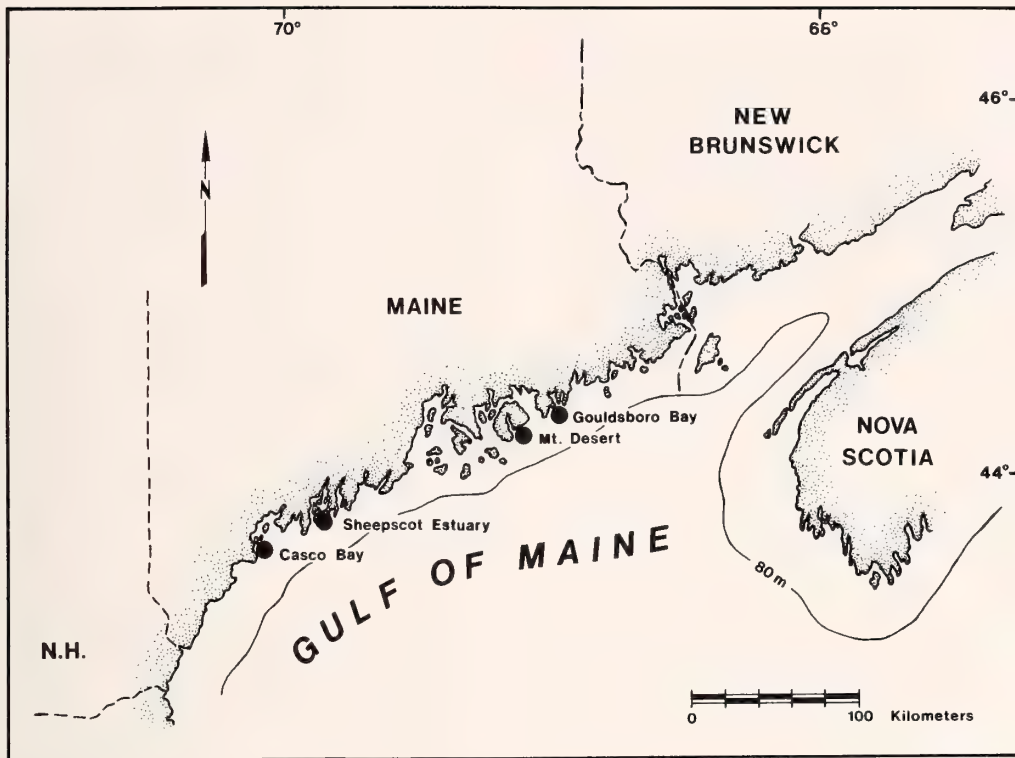


Figure 6

Distribution of *Sphenia sincera* Hanks & Packer, spec. nov., in the Gulf of Maine. Dots are points of actual collection; the 80-m contour bounds the inferred range (from Casco Bay to perhaps northeastern Nova Scotia) based on known habitat requirements.

The unique characteristics of *Sphenia sincera*—bright, clean, undistorted shell of distinct shape, solid calcification, and geographic remoteness from other species of *Sphenia*—are probably sufficient to prevent confusion with any other species in the genus. However, specific comparisons help to establish the precise differences between species and to define the new taxon.

Sphenia antillensis Dall & Simpson, 1901, appears to be the closest living species to *S. sincera* both in geographic location and its generally non-nestling existence. It has been reported from Puerto Rico (DALL & SIMPSON, 1901; WARMKE & ABBOTT, 1961), Brazil (RIOS, 1975), Surinam (RIOS, 1975), the Atlantic coast of Panama (ROSEWATER, 1975), and South Padre Island, Texas (ODE, 1971). Recent additions of *S. antillensis* to the collections of the U.S. National Museum of Natural History have extended its range northward. Specimens were found at Sebastian Inlet, Florida, in 1978 (USNM 836238), and at Cumberland Island, Georgia, in 1982 (USNM 819628). Even though *S. antillensis* is the only member reported to be living in sandy bottoms and having undistorted shells (DALL & SIMPSON, 1901; WARMKE & ABBOTT, 1961; RIOS,

1975), ODE (1976) mentions it as being a deformed species found in a nestling habitat. In addition, specimens in the U.S. National Museum of Natural History from worm reefs in Sebastian Inlet, Florida (USNM 836238), had the characteristic convoluted, distorted shells of a nestler. In any case, the shell of *S. antillensis* is quite distinct from *S. sincera* in having more acute umbones, a distinctly flattened anterior margin not curving regularly as in *S. sincera*, a broader posterior end, and an unusual concavity on the posteroventral portion of the shell, giving the shell a keeled shape. *Sphenia antillensis* has a yellow periostracum but, apparently, this is often missing.

LEWIS (1968) has recently described *Sphenia tumida* from the Pleistocene of Flagler County, Florida. Three other fossil species recorded from this region are *Sphenia dubia* (Lea, 1845), *S. attenuata* Dall, 1898, and *S. senterfeiti* Gardner, 1936. The first is from the Miocene of Virginia and North Carolina, the latter two from the Pliocene and Miocene of Florida respectively. *Sphenia sincera* differs in being larger and more regular in shape than *S. dubia* or *S. senterfeiti* and in being neither attenuated, tumid, nor rostrate as are *S. attenuata* and *S. tumida*. Of course, *S.*

sincera differs in being a living species, although ODE (1971, 1976) has reported a single valve of *S. tumida* found in Freeport, Texas, that might be recent.

Two species of *Sphenia* are found in the Eastern Pacific. They are *Sphenia luticola* (Valenciennes, 1846) and *Sphenia ovoidea* Carpenter, 1864. *Sphenia luticola* is apparently the most ubiquitous member of the genus on the Pacific coast, having been reported from Oregon to Peru (see KEEN, 1971; ABBOTT, 1974; REHDER, 1981; under the synonym *fragilis* H. & A. Adams, 1854). The shell is elongate and opaque, but not solid. The periostracum is dull yellowish-gray to brown and adherent, but the surface of the shell is somewhat nacreous and almost smooth, with indistinct annuli. The posterior is attenuated, truncate, and commonly twisted. Internally, the shell is white; the pallial sinus is slightly oblique and not large. The anterior adductor scar appears to be more ventrally displaced than in most other *Sphenia*. Although there is considerable variation in shell shape as a result of the nestling habit (KEEN, 1971; REHDER, 1981), this species can be separated from *S. sincera* by the yellowish-gray to brown periostracum, the attenuated posterior end, and the size and position of the adductor scars. *Sphenia ovoidea* has a small shell and occurs from the Aleutian Islands to Panama. The anterior end of this shell is ovally rounded and the shell bears a yellow, somewhat rugose periostracum. The posterior end is truncate and somewhat attenuated. The pallial sinus is large and deep, often reaching to the middle of the shell. The pallial line is quite pronounced, and this would appear to be a good distinguishing feature in separating the shell from *S. sincera*. ABBOTT (1974) lists *S. ovoidea* as a possible ecologic form of *Sphenia luticola*.

Sphenia sincera differs from the type species, *S. binghami*, in having a thin, deciduous periostracum rather than a heavy, thick, brown periostracum, and in having the posterior end undistorted, with the dorsal and ventral margins converging rather than nearly parallel as in *S. binghami*. This latter characteristic appears to be an excellent diagnostic feature, and nearly all *S. binghami* that have been examined or figured have a square posterior end. Juvenile shells exhibit this characteristic at the smallest sizes. Of course, some larger *S. binghami* become so distorted posteriorly that the square shape is masked, but it is still evident even in very twisted shells. *Sphenia binghami* has a thinly calcified posterior end, whereas the entire shell is evenly calcified in *S. sincera*. The umbones are usually situated less than one-third of the distance between the anterior and posterior ends—the umbones of *S. sincera* are located about one-third of the distance. The anterior end of *S. binghami* is obliquely truncate, whereas in *S. sincera* it is generally rounded. The adductor scars are larger in *S. binghami*; the posterior adductor scar is wider (height two-thirds of width), as compared to that in *S. sincera* (width two-thirds of height). YONGE (1951) reported that the siphons of *S. binghami* are short, whereas the siphons of *S. sincera* are comparatively long.

Sphenia coreanica Habe, 1951, described from the coasts

of Korea and Japan, is very truncate posteriorly, has a somewhat crenulated anterior and ventral margin, and has a discontinuous pallial line. This shell is so different from *S. sincera* that there is no possibility of confusing the two.

Identification of the species of *Sphenia* can be difficult because of their small size and often extreme distortion resulting from the nestling habit. The taxonomic status of some specimens remains uncertain, and the genus is in need of a thorough review in regard to taxonomy and distribution. However, each species has distinctive morphological features, and *Sphenia sincera* presents an idealized morphological ground plan that, by its perfection, separates the shell from other members of the genus.

Growth and age: Measurements of the increments between successive external shell annuli were used to determine growth rates. Although growth rings have been used to determine age and growth in mollusks, this method has several sources of error, because annuli can be caused by any source of arrested growth in addition to that resulting from low water temperature, including unusual environmental conditions, spawning, poor feeding conditions, predation, and changes in sediment structure (NEWCOMBE, 1935, 1936a; BROUSSEAU, 1979; MACDONALD & THOMAS, 1980). However, small, fast growing, short-lived mollusks appear to produce more discrete and predictable rings than others (PETERSEN, 1978; BROUSSEAU, 1979).

Specimens of *Sphenia sincera* collected in June of 1962 were held in laboratory trays, with flowing seawater at ambient local temperature, until February of 1963. Measurements of each annulus, and overall shell length, were made on 147 shells using the right, or largest, valve. Generally, three annuli were apparent, and can be interpreted from smallest to largest as (1) first winter check (1961–62), (2) check caused by collection and handling in June, and (3) second winter (1962–63) check. Usually, the final (second winter) check coincided with total length, but in some specimens new growth of about 0.1 to 0.2 mm width was noted. The mean length at the first winter check was 3.0 mm (range 1.1 to 4.6 mm), at the collection check 4.0 mm (range 2.4 to 6.1 mm), and at the final check 5.1 mm (range 4.1 to 7.1 mm). Since this mean ultimate size is similar to the mean size of natural populations, it is assumed that laboratory growth rates were comparable to growth in wild populations. Mean growth in one year, under the conditions described, was a little more than 2 mm in length. The fastest growth recorded for the period was 4.7 mm, and the slowest 0.6 mm. Slow growth was characteristic of clams that were small at the first winter check. Growth of *Sphenia sincera* is considerably less than that reported for *Mya arenaria* by various authors (BEDDING, 1907, 1916; PACKARD, 1918; NEWCOMBE, 1935, 1936b; DOW & WALLACE, 1951; MERRILL, 1959; STICKNEY, 1964a, b; HANKS, 1968, 1969; ARBUCKLE, 1982). *Mya truncata* also grows at a relatively slow rate, but even in the cold waters of coastal Greenland, the growth

rate appears to be twice as rapid as that of *Sphenia sincera* from Maine (PETERSEN, 1978).

The maximum length of *Sphenia sincera* appears to be about 1 cm; the largest specimen was taken in the Sheepscot region, had a total length of 9.9 mm, and had four shell annuli. Most individuals, however, apparently live only two to three years, and the mean size of all specimens measured was 5.4 mm.

DISCUSSION

Sphenia sincera has been collected from depths of 10 to 80 m in the Sheepscot region. Ninety percent of the dried sediment samples from this area consists of silt and clay. Specimens collected from the lower third of Gouldsboro Bay at 15 m depths were found in sediments consisting of 12% clay, 12% silt, and 76% sand, whereas collections taken 1.5 nautical miles (2.8 km) west of Petit Manan Island near the mouth of Gouldsboro Bay at depths ranging from 37 to 44 m were found in sediments that consisted on the average of 27% clay, 28% silt, and 45% sand (Packer, unpublished data). In both Gouldsboro Bay and the Sheepscot estuary, water temperatures near the bottom range from 1°C in the winter to 14°C in the summer. Salinities at the bottom are nearly uniform throughout the year at about 32‰. Mean tidal range for both areas is about 3 m. This presumably has little effect on populations of animals living at the depths *Sphenia* inhabits. Since the Gouldsboro populations seem to center outside the bay in offshore waters with depths to 63 m, the tidal effects are negligible as compared to those within the bay (ADEY, 1982). Most of the Sheepscot population centers in the mouth of the "lower estuary" (STICKNEY, 1959), where the major effect of tide is on current flow, both velocity and direction, and mixing (GARSIDE *et al.*, 1978; LARSEN *et al.*, 1980).

Most faunal associates of *Sphenia sincera* in the Sheepscot are members of a general *Nucula-Nephtys* dominated community described by HANKS (1964) and LARSEN (1979). Particularly abundant in these deeper waters are the bivalves *Nucula proxima* Say, 1822, *Nucula annulata* Hampson, 1971, *Thyasira gouldii* (Philippi, 1845), juvenile *Arctica islandica* (Linné, 1767), *Cerastoderma pinnulatum* (Conrad, 1830), *Yoldia limatula* (Say, 1831), and such polychaetes as *Sternaspis scutata* (Renier, 1807), *Nephtys incisa* Malmgren, 1865, and *Nephtys ciliata* (O. F. Müller, 1789). Tube-building amphipods, such as *Corophium* and *Ampelisca*, often produce thick mats of old tubes that lace the surface sediments in which the scale-worm *Hartmania moorei* Pettibone, 1955, may live as a commensal. In Gouldsboro Bay, the community is dominated by *Nucula* and the cumaceans *Diastylis sculpta* Sars, 1871, *Diastylis polita* (S. I. Smith, 1879), and *Eudorella pusilla* Sars, 1871, as well as such polychaetes as *Scoloplos acutus* (Verrill, 1873a) and *Prionospio steenstrupi* Malmgren, 1867. Outside the bay, *S. sincera* may reach a density of as much as 250/m², and is one of the dominant

soft-bottom invertebrates, along with *Nucula* and the polychaetes *Prionospio steenstrupi*, *Ninoe nigripes* Verrill, 1873a, and *Capitella capitata* (Fabricius, 1780) (Packer, unpublished data).

Major predators of these *Sphenia* populations are bottom-feeding cod, haddock, and flounder. Stomach contents of small cod and haddock, captured near the mouth of the Sheepscot River in June 1962, revealed that they were feeding almost exclusively on *Sphenia*. One small haddock (total length about 46 cm) contained over 400 specimens of *Sphenia*, with only a few other small mollusks (*Arctica* and *Clinocardium*). If the range of *Sphenia sincera* extends along the Maine coast, and if its abundance is as great as in the Sheepscot and Gouldsboro regions, it must be an important food for inshore groundfish populations. In addition to the extensive use as food for fish, *Sphenia sincera* is undoubtedly prey for many other animals. Three shells collected near Mt. Desert Island (USNM 172122) and several from Gouldsboro Bay were drilled by a gastropod. From the tapered edges of the small hole, it is believed that they were drilled by a naticid (CARRIKER, 1981), common predatory gastropods found in these waters.

Sphenia sincera has the morphological characteristics of a filter-feeding mollusk (YONGE, 1951) and could feed on materials similar to those utilized by *Mya arenaria*, such as phytoplankton (NEWCOMBE, 1935; STICKNEY, 1964a, b; ARBUCKLE, 1982). Specimens of *Sphenia sincera* collected in Maine were held in artificial seawater aquaria in the laboratory at Oxford, Maryland, from July to November 1967. During these 4 to 5 months the clams were offered weak suspensions of *Phaeodactylum* and *Chlorella*. Since mortalities were less than 10% during this period, it is assumed that the clams did feed, but we could not confirm that the algae were used. It is entirely possible that other microorganisms may have been nutritionally significant—there is some evidence that *M. arenaria* may be a deposit-feeder as well as a suspension-feeder (RASMUSSEN, 1973) as is true in such other bivalves as *Macoma balthica* (Linné, 1758) (BRAFIELD & NEWELL, 1961). This may also be the case for *Sphenia sincera*, since it appears that many benthic species are generalist feeders (MAURER *et al.*, 1979). *Sphenia sincera* may be more of a deposit than a suspension-feeder because it is found in high silt-clay sediments along with very large numbers of such other deposit-feeders as *Nucula proxima*. Deposit-feeders tend to be dominant in bottoms of these types because they destabilize the soft sediments and suffocate suspension-feeding organisms (SANDERS, 1958; RHOADS & YOUNG, 1970; LEVINTON, 1977). Also, selective deposit-feeders are most sensitive to the abundance of the clay-sized particles, a reflection of the availability of organic detritus in the fine-grained sediment. Greater amounts of organic matter permit larger bacterial populations that are a food source for deposit-feeders (SANDERS, 1958; DRISCOLL & BRANDON, 1973; LEVINTON & BAMBACH, 1975). In the Sheepscot and Gouldsboro regions abundant detritus is available from such macroalgae as *Ulva*, *Fucus*,

and especially *Ascophyllum* (ADEY, 1982) along with the seagrass *Zostera marina* Linné, 1753.

The habitats of *Mya arenaria* and *Sphenia sincera* are separated by difference in bathymetric preference; the former species rarely extends much below the low-tide level (THEROUX & WIGLEY, 1983), and the latter inhabits much deeper water, deeper than 10 m with greatest abundance below 30 m. Although it is difficult to retain the natural relation with the bottom surface in deep-water samples, individuals of *S. sincera* appear to have a similar orientation to juvenile *M. arenaria* of the same size; that is, the anterior end directed down and the posterior end with the siphons directed toward the surface. The burrows do not appear to be lined with mucus or other supportive material. Clams held in our aquaria rarely dug into sediments, or buried themselves partially, but this could be unusual behavior induced by the sediments (generally sandy) used, as it was extremely difficult to reproduce the typical sediment structure of the Sheepscot region in the laboratory. As a possible filter-feeder in such soft sediments, *Sphenia sincera* is restricted to the top 25 mm of sediment due to its short siphons, also evidenced by the prevalence of clams of this species in the stomachs of bottom-feeding fish. *Mya arenaria*, on the other hand, is a deep burrower, and in order to maintain an open tube through which its long siphons can be withdrawn and re-extended, it prefers to live in a more cohesive, stable substrate, such as muddy sand. STANLEY (1970) notes that young *Mya arenaria* living in soft mud are unable to maintain permanent tubes for their siphons.

Mya truncata is also found in the deeper waters of the Gulf of Maine (VERRILL, 1873) but not in dense populations. Specimens have not been taken in samples for this study or in other surveys (HANKS, 1961, 1964; LARSEN, 1979; THEROUX & WIGLEY, 1983). Scattered reports of *M. truncata* along the Maine, New Brunswick, Nova Scotia, and Gaspé coasts indicate that inshore populations are widely distributed and low in density. Adult *M. truncata*, obtained from the Maine coast and Canada, were all true *M. truncata* and not *Mya pseudoarenaria* Schlessch, 1931, which resembles *M. arenaria* (LAURSEN, 1966; BERNARD, 1979a, b; LUBINSKY, 1980; SIMONARSON, 1981). Extreme phenotypes of *M. truncata* have a superficial resemblance to *Sphenia sincera* (FOSTER, 1946), but this species of *Mya* has a smaller anterior tooth in the right valve (this tooth is not found in *M. arenaria*) and the anterior adductor scar extends farther ventrally than it does in *S. sincera*. Although *M. truncata* is generally subtidal in deep water along the southern part of the Gulf of Maine, it also occurs in shallow water and can be found intertidally on the northern part of the Maine coast and on Canadian shores (LUBINSKY, 1980) in all types of sediments, although it frequently prefers firm clay bottoms. René Lavoie (personal communication) of the Faculty of Science, Laval University, Quebec, P.Q., said that he found adult *M. truncata* valves still joined by the ligament—indicating fairly recent mortality—on the Gaspé shores of the St.

Lawrence. SMITH (1953) demonstrated that adult *Mya arenaria* decayed slowly after death, and that some remains of meat and adductor muscle were still evident after three months in summer and four months in winter. We can infer that the ligamentally joined *M. truncata* shells from the St. Lawrence had been dead for at least one year, and possibly much longer.

The evidence, therefore, indicates that *Sphenia sincera* occupies a habitat different from that of adult *Mya arenaria* and *Mya truncata*, that it does not compete for space with juvenile *Mya arenaria* which live mostly in shallow waters and intertidal regions, and that little competition can occur with juvenile *Mya truncata*, which are not common in offshore Maine waters near the southern limit of their distribution.

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An Anesthetic for Internal Operations on the Land Snail *Helix aspersa* Müller

by

DANIEL CHUNG

Museum of Zoology and Division of Biological Sciences,
University of Michigan, Ann Arbor, Michigan 48109

Abstract. An anesthetic solution consisting of 2% magnesium chloride and 0.01% succinylcholine chloride in combination was used to anesthetize *Helix aspersa* for internal operations. A dosage of 0.012 mg of succinylcholine per gram of snail tissue and 2.4 mg/g $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$ was injected into the hemocoel to produce a quick and pronounced anesthesia with a nearly 100% survival rate. The combined action of the two drugs at low dosages resulted in an anesthesia better than either drug alone at high dosages. At a higher dosage, the new anesthetic solution also worked on *Arion circumscriptus* and may be useful for operations on other land snails.

INTRODUCTION

A LARGE NUMBER OF agents is used for relaxing gastropods. RUNHAM *et al.* (1965) reviewed the effectiveness of a number of narcotizing agents used to relax snails before fixation in an extended position and anesthetics used for relaxing snails prior to operations. Proper relaxation must leave living snails in an extended position and insensitive to touch and to chemicals. Agents that have been tried on snails in recent years include CO_2 , hypothermia, dilute formalin, dilute seawater, menthol, propylene phenoxytol, ether, urethane, tricaine (MS-222), Stovaine, Nembutal (see RUNHAM *et al.*, 1965), succinylcholine chloride (BEE-MAN, 1968; BURTON, 1975), curare, Novocaine, Xylor-caine, methohexital sodium (BEEMAN, 1968), calcium-free seawater, Benzocaine, procaine hydrochloride (Novo-caine) (STIRLING *et al.*, 1984), manganese sulfate (YESCOTT & HANSEN, 1976), pentobarbital (MEIER-BROOK, 1976), magnesium chloride (numerous authors, including RUNHAM *et al.*, 1965; TURNER, 1976), Althesin, benzyl alcohol, quinaldine, xylazine (BOURNE, 1984), nicotine, dilute ethanol, and various combinations of these agents. Those reported to be useful for internal operations on gastropods include propylene phenoxytol, magnesium chloride, Nembutal/MS-222 (evaluated by RUNHAM *et al.*, 1965), CO_2 (BAILEY, 1969), Nembutal/ MgCl_2 (JEP-PESEN, 1976), and isotonic MgCl_2 (ROBERTS & BLOCK, 1982). BURTON (1975) reported that succinylcholine chloride was useful for anesthetizing *Helix pomatia* Linnaeus for tentacle excision. RUNHAM *et al.* (1965) reported that urethane and ether left snails imperfectly relaxed and was

found to be suitable only for external operations, although MALEK & CHENG (1974) recommended both agents with the use of physical retraction.

The effectiveness of many anesthetic agents has been frequently reported to vary widely among species, though a few agents, such as Nembutal and MgCl_2 , have been used successfully on numerous species.

I have tried various combinations and dosages of MgCl_2 , Nembutal (sodium 5-ethyl-5-[1-methylbutyl]-barbiturate, or pentobarbital sodium), MS-222 (ethyl m-aminobenzoate methanesulfonate, or tricaine), and succinylcholine chloride in an effort to obtain a quick, injectable anesthetic for internal operations on *Helix aspersa* Müller. Injection of Nembutal and MS-222 did not relax *Helix aspersa* well, so no further trials of MS-222 were conducted. The methods described by JEPPESEN (1976) and BURTON (1975) for *Helix pomatia* gave the most satisfactory results, but were either time-consuming and/or led to unacceptable mortality rates and difficulty during surgery. I report here a quick-acting anesthetic solution with a high survival rate that may also be useful for other large land snails. The results of some preliminary trials of injections of MgCl_2 , Nembutal, and succinylcholine chloride are presented to facilitate discussion of the effect of the working anesthetic solution.

MATERIALS, METHODS, AND TECHNIQUE

Preliminary Trials

Healthy adult and subadult specimens of *Helix aspersa* obtained from California were used to test various con-

Table 1

The dosage and evaluation of anesthetic solutions on *Helix aspersa*. Dosage is in mg of drug per gram of snail tissue (weight of whole snail minus weight of shell). Evaluation: good (G) for full anesthesia, fair (F) for partial anesthesia adequate for very quick surgery, unsatisfactory (U) for poor relaxation and high irritability of the snail, and no effect (NE) for no response to the injected solution. SChCl = succinylcholine chloride.

Solution	Approximate dosage	Num-ber of snails in-jected	Evaluation			
			G	F	U	NE
10% MgCl ₂	12.0 mg/g	11	1	3	7	
5% MgCl ₂	6.0 mg/g	11		2	9	
2% MgCl ₂	2.4 mg/g	10			10	
0.25% SChCl	0.30 mg/g	12			12	
0.05% SChCl	0.06 mg/g	13		3	10	
0.01% SChCl	0.012 mg/g	14			14	
0.25% Nembutal	0.30 mg/g	11			11	
0.1% Nembutal	0.12 mg/g	10			10	
2% MgCl ₂ /	2.4 mg/g	10			10	
0.1% Nembutal	0.12 mg/g					
2% MgCl ₂ /	2.4 mg/g	10	10			
0.05% SChCl	0.06 mg/g					
2% MgCl ₂ /	2.4 mg/g	98	98			
0.01% SChCl/	0.012 mg/g					
0.005% Strepto- mycin sulfate	0.006 mg/g					
0.05% Strepto- mycin sulfate	0.06 mg/g	9				9

centrations and combinations of MgCl₂, Nembutal, and succinylcholine chloride (Table 1). Snails weighing 4 to 7 g were injected through the thin body wall of the upper left region of the head-foot just below the mantle collar (the "nuchal" region). The snails were washed and allowed to crawl around until the shell could be lifted and tilted so that the "nuchal" region was exposed; the injection was then made into the hemocoel. Mild massage of the head-foot facilitated an even distribution of the anesthetic. All the snails of each group received approximately the same dosage. The effectiveness of the solution injected was judged by its ability to: (1) render the snail immobile and unresponsive to pinches on the side of the head-foot, (2) keep the snail completely insensitive for at least 10 min after the injection, and (3) wear off within one or two days. The anesthetic was judged to be good (G) if all these criteria were met, fair (F) if the criteria were met partly with the snail slightly reactive to touch, but relaxed enough for minor external or quick internal surgery, unsatisfactory (U) if none of the criteria were met or if the snail remained very reactive to pinches of the body wall, and with no effect (NE) if the snail showed no change or slowing of movement.

Working Anesthetic Solution and Technique

Ninety-eight healthy adult and subadult specimens of *Helix aspersa* were injected with approximately 0.4 to 0.7 mL of the following solution:

2% MgCl₂·6H₂O
0.01% succinylcholine chloride (Sigma Chem. Co., St. Louis, Missouri)
0.005% streptomycin sulfate
w/v, in distilled H₂O.

The solution was prepared immediately before use and remained effective for one day. The snails were injected with a volume that delivered an approximate dosage of 0.012 mg of succinylcholine chloride per gram of snail tissue (weight of whole snail minus weight of shell). This amounted to about 0.65 mL for an average-sized snail with a tissue weight of 5.4 g (6.3 g for the whole snail). The volume of anesthetic was roughly proportional to body weight. This seemed reasonable considering the fact that respiration in helicids has been reported to be nearly proportional to weight (see GHIRETTI & GHIRETTI-MAGALDI, 1975). The weight of the snail tissue was calculated from the weight of the whole snail using a regression line previously obtained from 38 specimens of *H. aspersa*: $Y = 0.884X - 0.155$, where Y is tissue weight in grams (weight of whole snail minus weight of shell) and X is weight of the whole snail in grams; $r = 0.975$, Y ranging from 3.5 to 8.0 g. Snails were injected in the manner described above. In order to check for the possible anesthetic effect of the antibiotic streptomycin sulfate, a few snails were injected with a 0.05% streptomycin solution, which was 10 times the concentration in the anesthetic solution. Antibiotics have been reported to have an anesthetic effect in mammals (see GILMAN *et al.*, 1980).

Survival of snails undergoing surgery seemed to depend on retention of body fluids during surgery and on allowing sufficient rest during recuperation. For surgery on the terminal genitalia, the head-foot of the snail was placed on a dissection dish so that the shell lay in a shell-shaped depression in the wax. With the shell lying in a depression, most of the body fluids remained in the visceral hemocoel, and loss of fluid in short operations was usually less than 0.2 mL. The incision was sutured with fine surgical silk using a No. 2 eye type, half-curved needle (George Tiemann & Co., New York). Snails were then placed into clean, dry containers and allowed to estivate for one week. The sutures were removed after this period of estivation. Two snails that appeared dehydrated and ill after surgery were put into containers lined with moist soil and given carrots to feed on for one week before the sutures were removed. The operations performed included excision of parts of the genitals and implantation of tissue from other snails into the hemocoel. The fully recovered snails were kept in soil-lined containers and fed carrots.

Fifteen specimens of *Arion circumscriptus* Johnston were injected to determine the effect of the working anesthetic

solution on other snails. Seven of these slugs were cut open and then sutured; the other eight were undisturbed. The slugs were given a dosage of about 0.25 mg succinylcholine per gram body weight, about 20 times the dosage for *Helix aspersa*; this dosage was necessary for complete anesthesia during surgery. The slugs weighed 0.45 g on average and had a maximum body length of 25 mm. Anesthetized slugs were put into containers with moist paper towels until they recovered. The anesthetic solution was also tried as a soaking solution on 10 specimens of *Biomphalaria glabrata* (Say). I observed the state of anesthesia but did not operate on these snails.

RESULTS

Preliminary Trials

The results of the preliminary trials are shown in Table 1. The effect of each solution was generally very uniform, even though the numbers of snails injected in these preliminary trials were small. Snails injected with the $MgCl_2$ solution recovered quickly from its effects—all were able to crawl within 30 min after injection. Snails receiving a 10% solution showed a wide range of reactions; most snails remained sensitive to pinches, though some remained fairly insensitive long enough for quick internal operations. Those receiving a 5% solution writhed when pinched on the side of the head-foot and began to crawl again 15 min after the injection. Those snails receiving a 2% solution never became completely anesthetized and continuously writhed slowly. Only one injection of the 32 snails receiving the $MgCl_2$ solutions resulted in a rating of good (G). Snails injected with Nembutal never became fully anesthetized. Those injected with the 0.25% solution slowly withdrew into the shell or writhed when touched. Those injected with the 0.1% solution writhed slowly and continuously; they appeared to be trying to crawl but seemed unable to coordinate their movements.

Snails injected with different concentrations of succinylcholine chloride showed an odd trend. Those receiving high dosages (0.25%) withdrew their heads after injection and remained highly reactive to light touch thereafter. Those receiving a lower dosage (0.05%) became insensitive to touch for 2 to 4 min after injection, long enough for quick external operations. Snails injected with the lowest dosage (0.01%) were insensitive for only about 1 to 2 min and subsequently recovered. None of the injections of 39 snails receiving the succinylcholine chloride injections was rated as good (G).

Those snails that received a solution of 2% $MgCl_2$ /0.01% Nembutal became limp and extended, but writhed when pinched. Snails injected with a solution of 2% $MgCl_2$ /0.05% succinylcholine chloride became fully anesthetized long enough for operations. The nine snails injected with 0.05% streptomycin sulfate showed no slowing of movement or narcosis of any kind.

All snails recovered the ability to crawl within 24 h after injection. All snails became reactive to stimuli many

hours before they could crawl again, except for those that received $MgCl_2$.

Differences between different dosages for any one drug are not statistically significant because of low sample number and an insufficient number of ranks, but the differences in the effects between the $MgCl_2$ /succinylcholine mixture and the pure $MgCl_2$ or pure succinylcholine solutions (all dosages pooled) are significant, since they show almost no overlap in their effects (as evaluated in Table 1).

Working Anesthetic Solution

The working anesthetic solution of 2% $MgCl_2$, 0.01% succinylcholine chloride, and 0.005% streptomycin sulfate gave excellent results during operations on 98 snails. The revival rate after the operation and survival rate after one week were both 100%.

The snails anesthetized by this solution became limp and flaccid within a few seconds after injection. They remained insensitive to pinches and touch for at least 10 min after injection. After this time, the tentacles and labial region first regained sensitivity to stimuli, and snails pinched in these places showed some snout retraction momentarily. More than 50% of the operated snails started to crawl again within 6 h after injection, and all snails had recovered the ability to crawl within a day after the injection.

The combination of the two drugs in the working solution worked better than either drug alone, even at high dosages. A somewhat stronger dosage of succinylcholine (0.05%) when used with $MgCl_2$ (see Table 1) was also effective and may be useful for longer operations.

While under the anesthetic, the snails stopped secreting mucus and the pneumostome stopped its rhythmic opening and closing. During operations, the cut surface of the incision on the body wall curled inward slightly and the region around the incision shrank somewhat. This local response could not be abolished at higher dosages, but it did not cause much difficulty with the surgery and helped reduce loss of blood. Blood loss during surgery, determined by measuring the volume of hemolymph remaining in the dissection dish, remained less than 0.2 mL and averaged 0.05 mL, though the volume of fluid loss would depend on the type of surgery being performed.

Arion circumscriptus injected with the working anesthetic solution at a dosage 20 times that given to *Helix aspersa* became fully anesthetized within a few seconds. The local skin tightening response was more pronounced than in *H. aspersa*, probably due to the greater muscularity of the body wall in the slug. The slugs began recovering from the anesthesia within 30 min after injection. All 15 slugs were able to crawl 2 h after injection.

The anesthetic solution could not be used as a soaking solution on the basommatophoran *Biomphalaria glabrata*. These snails slowly withdrew deep into their shells and would not re-emerge until restored to freshwater. They

could not be injected, because they remained too sensitive to touch.

DISCUSSION

The new anesthetic solution reported here appears to work better than other anesthetics reported for *Helix aspersa*. The combination of succinylcholine chloride and $MgCl_2$ acts better than either drug alone, perhaps because of potentiation of succinylcholine by magnesium ion. Of the solutions tried in the preliminary trials, 10% $MgCl_2$, 0.05% succinylcholine chloride, and to a lesser degree 5% $MgCl_2$ appeared to be suitable for quick or external surgery. The contractions that occurred during surgery on snails given these solutions were manageable for a short period immediately after injection. However, contractions of the snails increased blood loss and difficulty of surgery. RUNHAM *et al.* (1965) reported a survival rate of 85% one week after surgery on *Helix aspersa* injected with 10% $MgCl_2$ (I estimate a dosage of about 5.8 mg $MgCl_2$ per gram of snail tissue from their figures). JEPPESEN (1976) reported about an 80% survival rate six months after surgery on *H. pomatia* anesthetized by soaking in a 0.1% Nembutal solution followed by injection of up to 1 mL of 10% $MgCl_2$. BURTON (1975) used a dosage of 0.1 mg to 0.017 mg succinylcholine chloride per snail for tentacle excision; this is a dosage of roughly 0.01–0.17 mg/g, if *H. pomatia* tissue weighs an average of 10 g. I estimate that BEEMAN (1968) used a dosage of 0.013 mg/g of succinylcholine to produce a state of reversible narcosis in *Aplysia*. These dosages are comparable to or higher than the dosages of these drugs in the working anesthetic used on *H. aspersa*—0.012 mg/g succinylcholine, 2.4 mg/g $MgCl_2$.

The combination of $MgCl_2$ and succinylcholine produces a pronounced anesthesia. The mechanism for this action in *Helix aspersa* is unknown. However, it is known that in man and cats magnesium ion potentiates the effect of succinylcholine and other muscle relaxants (MORRIS & GIESECKE, 1968; GIESECKE *et al.*, 1968; GHONEIM & LONG, 1970). Magnesium ion has been demonstrated to reduce the release of acetylcholine at the neuromuscular junction in vertebrates (DEL CASTILLO & ENGBAER, 1954) in a manner similar to that produced by lack of calcium ion (see HUBBARD, 1973). Succinylcholine is an antagonist to acetylcholine in neurons of the subesophageal ganglia of *Helix aspersa* (WALKER & HEDGES, 1967) and is known to produce a neuromuscular block in humans and vertebrates by blocking the action of acetylcholine on the post-synaptic membrane of the neuromuscular junction (see GILMAN *et al.*, 1980). Concurrent application of the two drugs produces an additive effect (GIESECKE *et al.*, 1968; GHONEIM & LONG, 1970). In contrast, I could find no indication of an increase in effect when Nembutal (a barbiturate) and $MgCl_2$ were used together. In humans, barbiturates are hypnotics that work on the central nervous system and have almost no peripheral effect (see GILMAN

et al., 1980). I have used a combination of Nembutal, $MgCl_2$, and succinylcholine chloride injected immediately after mixing for operations on more than 250 *H. aspersa*, with a survival rate of nearly 100%, but such a combination was no more effective than the solution not containing the Nembutal.

The interaction between magnesium ion and succinylcholine may be undesirable in humans, but it may be useful to investigators working on snails. The use of agents with similar action may explain the effectiveness of the narcotizing technique reported by STIRLING *et al.* (1984). Their sequential use of calcium-free seawater, $MgCl_2$, and procaine hydrochloride (Novocaine) on veligers may affect nerve endings. In vertebrates, calcium ion functions to release acetylcholine at the synapse and is antagonized by magnesium (see HUBBARD, 1973), and procaine makes nerves less permeable to ions.

The test of the new anesthetic on *Biomphalaria glabrata* indicates that the anesthetic cannot be used as a soaking solution and probably must be injected to anesthetize the snail and simultaneously extend the body from the shell. Extension of the head-foot from the shell is important in operations on shelled gastropods. In slug forms, anesthesia may not be necessary, provided that physical immobilization is used. HARLEY & HARLEY (1973) operated on large *Aplysia californica* without anesthesia and obtained a good survival rate if the weight loss during the operation was kept below 15% of the pre-operative value. A good anesthetic must leave the snail well extended from the shell and prevent major contraction during surgery to reduce blood loss. The successful use of the new anesthetic on *Arion circumscriptus* indicates that the anesthetic solution might be used successfully on other land snails.

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Two New Northeastern Pacific Gastropods of the Families Lepetidae and Seguenziidae

by

JAMES H. McLEAN

Los Angeles County Museum of Natural History, 900 Exposition Boulevard,
Los Angeles, California 90007

Abstract. Two new deep water gastropods from the northeastern Pacific are described. In the family Lepetidae, *Iothia lindbergi*, broadly distributed at continental shelf depths, Vancouver Island, British Columbia, to Cabo San Quintín, Baja California; and in the Seguenziidae, *Seguenzia quinni*, from abyssal depths off Oregon.

INTRODUCTION

TWO SPECIES ARE described below, preliminary to inclusion in an account of the archaeogastropods of the northeastern Pacific from Alaska to Baja California. In that work the rhipidoglossate species are to be treated by McLean and the docoglossate species by Lindberg.

Type material is placed in the Los Angeles County Museum of Natural History (LACM), the National Museum of Natural History, Washington, D.C. (USNM), the California Academy of Sciences, San Francisco (CAS), and the National Museum of Canada, Ottawa (NMC).

Family LEPETIDAE Dall, 1869

Genus *Iothia* Gray, 1850

Iothia lindbergi McLean, spec. nov.

(Figure 1)

"*Lepeta caecoides* Carpenter," SMITH, 1963:160.

"*Lepeta (Iothia) fulva* (Müller)," McLEAN, 1966:126, pl. 4, figs. 17-21.

Description: Shell (Figure 1) medium sized for genus (maximum length 6.2 mm), thin, translucent white; anterior slope concave to straight; posterior slope convex. Apex one-fourth shell length from anterior margin, eroded in mature specimens; protoconch retained in specimens under 2 mm in length, narrow, erect, non-spiral, posteriorly projecting. Fine concentric growth lines evident in shells under 2 mm long. Radial sculpture of 25 to 35 irregularly spaced ribs of unequal strength; rib interspaces broad, up to 5 times width of ribs; ribs imbricate, pustulose; pustules broader than high; concentric growth irreg-

ularities showing in interspaces. Interior glossy, muscle scar faintly marked.

Dimensions: Length 6.2, width 4.8, height 2.1 mm (holotype). The holotype is the largest specimen examined.

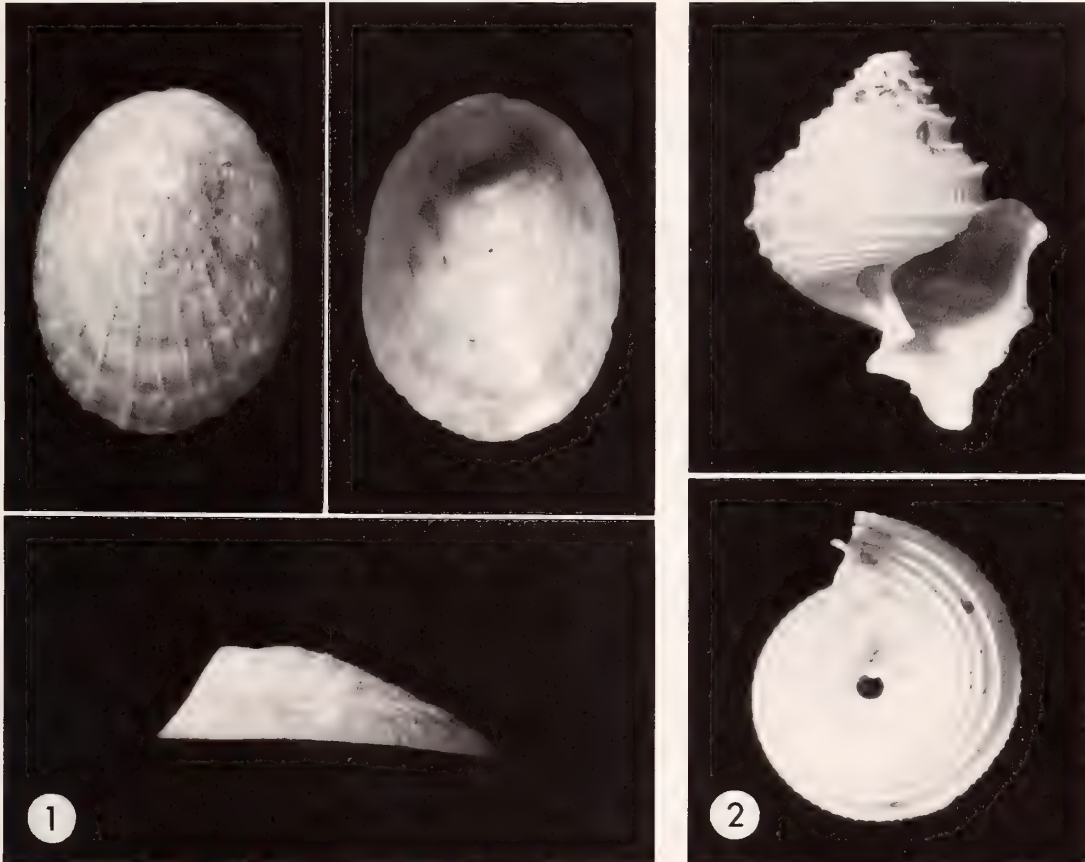
Type locality: 183 m (approximately 100 fm) on granite boulders, 6 miles (9.6 km) W of Point Pinos, Monterey Co., California (36°39'N, 122°01'W).

Type material: 6 specimens from the type locality dredged by James H. McLean, R/V *Tage* (Hopkins Marine Laboratory): holotype and one paratype, 17 November 1960; 4 additional paratypes, 2 March 1961. Holotype LACM 2063, 2 paratypes LACM 2064, 1 paratype CAS 050118, 1 paratype USNM 784749, 1 paratype NMC 86715.

Referred material: 17 lots of this species are represented in the LACM collection, ranging from the north end of Graham Island, Queen Charlotte Islands, British Columbia, to Islas San Benito, Baja California, dredged on rocks in depths from 90 to 300 m. Intermediate localities include—British Columbia: off the north end of Vancouver Island; Washington: off Cape Flattery; California: off Davenport, Santa Cruz County; off Santa Rosa Island; off Catalina Island; off Cortez Bank; Baja California: off Cabo San Quintín. There is a single LACM record taken by scuba diving: one dead shell in rubble at 51 m on Cordell Bank, Marin County (37°59.1'N, 123°25.5'W), Robert W. Schmieder, 8 October 1983.

Comparisons: *Iothia lindbergi* is smaller-shelled and lacks the reddish orange coloration of the northeastern Atlantic *I. fulva* (Müller, 1776).

Remarks: Earlier (McLEAN, 1966) I could not find suf-



Explanation of Figures 1 and 2

Figure 1. *Iothia lindbergi* McLean, spec. nov. Exterior and interior (anterior at top), and lateral (left side) views of holotype. Length 6.2 mm.

Figure 2. *Seguenzia quinni* McLean, spec. nov. Apertural and basal views of holotype. Height 7.6 mm.

sufficient grounds to separate the new species from *Iothia fulva* in the northeastern Atlantic. However, the northeastern Pacific species is now known from a sufficient number of lots to show that it never has a trace of the red-orange coloration usual in *I. fulva* and does not reach the size known for *I. fulva*. (The largest examined specimen of *I. fulva* is 8.2 mm in length; LACM, Gullmar Fjord, Sweden.) In view of these differences, and the greatly disjunct distribution, with no records of the genus in Alaska or the North American Arctic Ocean, a separate name for the northeastern Pacific species is warranted. No radular differences between the two species were detected, the radula being more useful as a generic than specific character in this genus.

Etymology: The name honors David R. Lindberg, of the University of California, Berkeley.

Family SEGUENZIIDAE Verrill, 1884

Genus *Seguenzia* Jeffreys, 1876

Seguenzia quinni McLean, spec. nov.

(Figure 2)

Description: Shell large for genus, up to 7.6 mm in height, higher than broad, narrowly umbilicate, thin, translucent white; interior and exterior surfaces with pink and green iridescence. Protoconch and first teleoconch whorl missing in the two known specimens. Remaining teleoconch whorls 6, evenly expanding. Primary spiral sculpture of three narrow, projecting keels—subsutural keel, which covers peripheral keel of preceding whorl, shoulder keel, and peripheral keel. Area between subsutural keel and shoulder keel concave at first, becoming slightly convex on final whorl; area between shoulder keel and peripheral keel concave at first, becoming straight on final whorl. Base evenly convex, with 10 spiral cords; those closest to peripheral keel and umbilicus more broadly spaced than other basal cords. Secondary sculpture of numerous, sharp, evenly spaced collabral riblets, and finer, microscopic, spiral threads. Collabral riblets traversing primary spiral

cords, forming fine, sharp nodes. Spiral threads present on spire and on base, except near umbilicus; spiral threads traversing axial riblets. Umbilicus narrow, bordered by projecting keel, faintly traversed by axial riblets. Outer lip thin, posterior sinus deep, bordering lip flared in mature stage. Parietal glaze thick enough to obliterate secondary sculpture but not primary spirals of base. Inner lip moderately thick, flared over umbilicus, strongly flexed at base to form strong columellar spur. Lip flared to left (in apertural view) anterior to columellar spur; lip also flaring to produce broad anterior canal.

Dimensions: Height 7.6, diameter 6.0 mm (holotype); height 7.3, diameter 5.9 mm (paratype).

Type locality: 3900 m, Tufts Abyssal Plain, 452 miles (723 km) W of Cape Foulweather, Lincoln Co., Oregon (45°02.0'N, 134°42.2'W).

Type material: One specimen from type locality, collected by the R/V *Yaquina*, Oregon State Univ. sta. BMT 306, 9 October 1972. Holotype LACM 2065. 1 paratype USNM 784750, from 2826 m, Cascadia Abyssal Plain, 144 miles (230 km) W of Cape Foulweather, Lincoln Co., Oregon (44°53.5'N, 127°27.5'W), collected by the R/V *Cayuse*, Oregon State Univ. sta. BMT 332, 4 November 1973.

Both specimens are now preserved dry; deeply retracted soft parts are visible through the translucent shell. Except for the slight difference in size, the two specimens are identical; both have 10 basal cords.

Referred material: Known only from the holotype and single paratype.

Comparisons: This is the only eastern Pacific *Seguenzia* to have strongly flaring borders to the anterior and posterior canals and to have a pronounced development of the columellar spur. Compared to other eastern Pacific species, *S. quinni* has spiral and axial sculpture like that of *S. stephanica* Dall, 1908, but that species is not umbilicate and lacks the strongly flaring anterior and posterior canals. The umbilicus and flared aperture of *Seguenzia quinni* resembles that of "*Seguenzia* n. sp.," from the Philippines (QUINN, 1983b, fig. 1), which differs in having a more acute spire angle and fewer spiral cords on the base. *Seguenzia textilis* MARSHALL (1983:242, figs. 3F-I), from the Tasman Basin, is smaller and has less pronounced axial riblets.

Remarks: Three other seguenziids (*Seguenzia stephanica*

Dall, 1908, *S. megalococoncha* Rokop, 1972, and the recently described *Carenzia inermis* Quinn, 1983) are also known at abyssal depths on the Cascadia Abyssal Plain off Oregon (LACM). However, none of these species is represented in material taken from the Tufts Abyssal Plain (type locality of *S. quinni*), west of the Juan de Fuca Ridge and the Blanco Fracture Zone. Infaunal biomass is richer on the Cascadia Plain (GRIGGS *et al.*, 1969; CAREY, 1981).

Etymology: Named after James F. Quinn, Jr., of the State of Florida Department of Natural Resources, St. Petersburg, who has recently reviewed the genera of the superfamily Seguenziaceae.

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NOTES, INFORMATION & NEWS

Soviet Contributions to Malacology in 1979

by

MORRIS K. JACOBSON

AND

KENNETH J. BOSS

Museum of Comparative Zoology,

Harvard University,

Cambridge, Massachusetts 02138

INTRODUCTION

We herein continue to list, as we have in past years, the Russian malacological papers abstracted in the 1979 Referativnyy Zhurnal (see Veliger 22(4):392 for the last listing and reference to previous ones). The delay in producing this bibliographic service was occasioned by the reluctance of the junior author to carry on after the unanticipated death of the senior author; however, a number of colleagues remarked on the utility of this list. Further, it would seem wise to attempt to keep abreast of some of the advances proposed in the Russian malacological literature. Often there are revolutionary revisionary works that completely alter the usually accepted taxonomic schemes and sometimes they follow quickly on the heels of those only previously proposed by Soviet researchers; this year proves no exception!

We have generally followed the categorical arrangement as utilized in the Referativnyy Zhurnal; however, we have not included the titles of abstracts of malacological papers published as part of the XIV Pacific Science Congress because these have been recently reviewed by LINDBERG (1984, Veliger 26(4):334).

Among the works listed this year, three are of particular importance and we provide somewhat more detailed abstracts for them: Shileiko's review of the systematics and classification of the terrestrial pulmonates (Geophila); Skarlato & Starobogatov's re-study of the classification of the Bivalvia in which once again we see several modifications and alterations in previous systems, especially in the establishment of new higher taxa and the elevation of previous taxa to higher rank; and finally, Minichev & Starobogatov's reclassification of the Class Gastropoda, which is subdivided by them into eight subclasses. The first two of the papers will appear in edited English translations in Special Occasional Publications published by the Mollusk Department, Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138.

Several other noteworthy contributions deserve mention: Sirenko's review of the Leptochitonidae, Lus' description of new taxa in the buccinids, and Moskalev's

review of the Lepetellidae, which has been translated through the auspices of C. S. Hickman, University of California-Berkeley, Department of Paleontology, Berkeley, CA 94720.

Important papers on the biology of squids, especially the ommastrephids, appeared by Nesis, Nigmatullin, and their colleagues.

Likharev & Viktor, acknowledged experts on terrestrial slugs, have studied the parallelisms and convergences in the evolution of the slug condition in different phyletic lineages. Zharkova also noted convergent loss of photosensitive organs and vision in deeper water marine gastropods.

Utilizing electrophoretic analyses, Logvinenko & Kodolova show the genetic distinctness of the margaritiferids from the unionids (*Unio* and *Anodonta*); a translation of this paper has been prepared through the efforts of Mr. Doug Smith, University of Massachusetts, Amherst, MA 01002. Another work involving electrophoretic techniques is that of Nikiforov who showed that what was considered by some as three separate species of oysters in the western Pacific is in fact only a single species.

Dr. Robert Robertson of the Academy of Natural Sciences of Philadelphia helped us to obtain an issue of the Referativnyy Zhurnal that was missing in the MCZ Library. Mrs. Robert Britz carefully typed the manuscript.

Abbreviations and acronyms we have used are:

- 2SC—2nd Vses. konf. po biol. shel'fa, Sevastopol. (Second all Union conference on the biology of [continental] shelves, Sevastopol).
- BMV—Biologiya Morya (Marine Biology, Vladivostok).
- ES—English summary.
- GZ—Gidrobiologicheskii Zhurnal (Hydrobiological Journal).
- NDVS—Nauch. Dokl. Vyssh. Shkol. Biol. Nauk. (Scientific Reports of the Higher Educational School for Biological Sciences, USSR).
- PDM—Promysl. dvustvorchat. mollyuski-midii i ikh rol' v ekosistemakh, Leningrad. (Commercial bivalve molluscan mussels and their role in the ecosystem, Leningrad).
- SRF—Nauch. Soobshch. Inst. Biol. Morya. Dal'nevost. Nauch. Tsentr. (Scientific Reports of the Institute of Marine Biology, Far Eastern Scientific Center. Acad. Sci. USSR).
- TIO—Trudy Instituta Okeanologii. Akademiya Nauk SSSR. (Transactions of the Institute of Oceanology, Academy of Sciences, USSR).
- TZI—Trudy Zoologicheskogo Instituta. (Transactions of the Zoological Institute of the Academy of Sciences of the USSR, Leningrad).
- ZEBF—Zhurnal Evolyutsionnoi biokhimii i fiziologii. (Journal of evolutionary biochemistry and physiology).
- ZOB—Zhurnal Obshchey Biologii. (Journal of General Biology).
- ZZ—Zoologicheskii Zhurnal. (Zoological Journal).

GENERAL

BELIAKOVA, YU. V. 1979. On the molluscan fauna of Central Kazakhstan. Fauna ekol. i zoogeog. gel'mintov zhivot. Kazakhstana (The fauna, ecology and zoogeography of helminth animals of Kazakhstan). Inst. zool. Akad. Nauk KazSSR, Alma Ata. 1978, pp. 44-45.

[In this region, related to the Volga-Ural and Irtysh provinces of the Euro-Siberian Palearctic subregion, 58 species of freshwater mollusks are known.]

BERGER, V. YA. 1979. The functional morphological basis of euryhalinity in marine mollusks. ZOB 40(1):93-103(ES).

[The problem of various mechanisms of osmotic tolerance and resistance to changes in salinity in marine mollusks is discussed.]

BERGER, V. YA., N. M. KOVALEVA, O. YU. MIKHAILOVA, YU. V. NATOCHIN & V. V. KHLEBOVICH. 1979. The influence of inhibitors on the ionic contents and size of muscle cells in marine mollusks. BMV, no. 4, pp. 47-53.

[Physiological experiments with *Mytilus edulis* and *Littorina littorea* showed variant effectiveness of sodium uptake by different chemicals.]

GOROKHOV, V. V. & V. S. OSETROV. 1978. Molluscicides and their application in rural industry. Kolos: Moscow. 224 pp.

[Designed for the use of agronomists and veterinarians, this book describes the method of application of special chemicals and their effect on the fauna and flora.]

KHOKHUTKIN, I. M., S. V. SHUTOV & V. N. OL'SHVANG. 1978. A more precise determination of the (zoogeographical) regions of continental mollusks in connection with a study on the biology of birds. Fauna, ekol. i izmenchivost' Zhivotnykh (Fauna, ecology and variability of animals), Sverdlovsk, p. 10.

LIKHAREV, I. M. 1979. Mollusks: fundamental results of their investigation. 6th All Union Meeting for the study of mollusks. Leningrad, 7-9 Feb. 1979. Leningrad. Nauka (Science Press), 263 pp.

LUKIN, A. K. 1979. On the freshwater molluscan fauna of the fluvial waters of the Saratov Region. Trudi Saratov. nauch. Vet. St. 13:51-56.

NATOCHIN, YU. V. & V. YA. BERGER. 1979. Ionic composition of molluscan cells: evolutionary and ecological aspects. ZEBF 15(3):295-302(ES).

[Despite sharp changes in intracellular sodium as cells adjust to various ambient salinities, intracellular potassium concentrations remain essentially constant.]

NISTRATOVA, S. N. 1979. On the change of cardiac sensitivity to acetylcholine during spawning in marine mollusks. ZEBF 15(5):508-512(ES).

[A correlation between the sensitivity of cardiac muscles to acetylcholine and the state of the reproductive system was discovered in 5 species of marine mollusks. It is shown that during the secretion of ripe sexual products, there is a considerable increase of sensitivity to the mediator acetylcholine from a threshold concentration of normally 10^{-9} to 10^{-15} or 10^{-17} molar at spawning.]

STADNICHENKO, A. P. 1979. Survey of Crimean freshwater mollusks. Vestnik zoologii, no. 1, pp. 14-19.

[35 species of gastropods and bivalves occur, of diverse geographical affinities, but Palearctic and Euro-Siberian species predominate.]

APLACOPHORA

IVANOV, D. L. 1979. The structure and functional morphology

of *Chaetoderma* (Mollusca, Caudofoveata) radular apparatus. ZZ 58(9):1302-1306(ES).

[A new terminology for the parts of the radula of *Chaetoderma* is proposed, based primarily on function. A critical analysis of the views of various students of the structure, provenience, and evolution of the radular apparatus is provided.]

POLYPLACOPHORA

SIRENKO, B. I. 1979. On the composition of the Leptochitonidae Dall 1889 (=Lepidopleuridae Pilsbry 1892) (Polyplacophora) and description of a new bathyal species. TZI 80:116-121.

[The status of *Leptochiton*, *Lepidopleurus*, *Deshayesiella*, *Hanleyella*, and *Oldroydia* is reviewed. The first four taxa are genera of this family and a diagnosis of each is offered. *Oldroydia* is a subgenus of *Deshayesiella*. Most chiton species lacking an insertion plate should be in *Leptochiton*. *Leptochiton batialis* from 1450-2500 m near the southern Kurile Islands and Japan is described as new.]

GASTROPODA, GENERAL

ALYAKRINSKAYA, I. O. 1979. On the mobilization of calcareous compounds in the shells of some gastropods. ZZ 58(5):648-654(ES).

[The quantity of calcium in the hemolymphs is increased in *Viviparus viviparus* in drought conditions and in *Helix pomatia* during hibernation and aestivation as well as at the time of egg laying. This promotes the buffering capacity of the hemolymph, which is essential under conditions of difficult extremes.]

MINICHEV, YU. S. & YA. I. STAROBOGATOV. 1979. Gastropod subclasses and their phylogenetic relationships. ZZ 58(3):293-305(ES).

[It is proposed to divide the class Gastropoda into 8 subclasses: Cyclobranchia (as outlined by GOLIKOV & STAROBOGATOV, 1975); Scutibranchia (as outlined by the same authors but with the addition of Loxonematoidea and the removal of Macluritidae, Ecculiomphalidae, and Onychochilidae); Pectinibranchia (as outlined by the same authors but with the exclusion of Pyramidellimorpha); Divasibranchia (Siphonariidae and Macluritida with families Macluritidae, Ecculiomphalidae, and Pelagiellidae); Dextrobranchia (as of MINICHEV & STAROBOGATOV, 1975, but with the addition of Order Onychochilida, a new order with the single family Onychochilidae); Pulmonata (in its usual extent, but with the addition of Subulitoidea and Vellainellidae but without Siphonariidae, Onchidiidae s. lato, Rhodopidae, and Soleolifera); Opisthobranchia (as of MINICHEV & STAROBOGATOV, 1975, but excluding Ringiculidae) and Sinistrobranchia, new subclass, which consists of 3 superorders and 5 orders: Superorder Architectonicoida with order Architectonicida (superfamily Architectonicoida, Mathildoidea, Nerineoidea) and order Epitoniida (superfamily Epitonioida, Janthinoidea); superorder Melanelloidea with order Melanellida (superfamily Pseudomelanoidea, Trochaclidoidea, Acidoidea, Melanelloidea); superorder Pyramidelloidea with orders Ringiculida (family Ringiculidae) and Pyramidellida (superfamily Pyramidelloidea). The diagnosis of each subclass is provided, the evolutionary processes leading to their characteristic features are discussed together with their phylogenetic relationships.]

SOKOLOV, V. A. & V. A. KOVALEV. 1979. The sensory system of gastropod statocysts. Sensor. sistemi i mekhanizmi zreniya. Nov. metodi issled. (Sensory system and the mechanics of vision. New investigative methods). Leningrad. pp. 136-148.

[SEM and electrophysiological data permit an analysis of how statocysts detect the gravitational field.]

GASTROPODA, PROSOBRANCHIA

- ARAKELOVA, E. S. 1979. The influence of temperature and size on the metabolic rate in *Melanopsis praemora* L. (Pectinibranchia). Eksperim. i polev. issled. biol. osnov. produktivn. ozer. (Experimental and field studies of the basic biological productivity in lakes.) Leningrad. pp. 169-180.
[Rate doubles with 10° increases (between 10° to 27°C).]
- BERGER, V. YA. 1978. A study of salinity adaptations in *Littorina sitchana*, with special reference to the evolution of the genus *Littorina*. ZZ 57(12):1786-1789(ES).
[*Littorina sitchana* has a high salinity tolerance but low resistance to freshwaters. The penetration of the genus into brackish water habitats in the north Atlantic was facilitated by the high osmotic tolerance of the ancestral Pacific form.]
- BERGER, V. YA. 1978. Euryhalinity and the evolution of *Littorina*. Morfol. sistematika i evolyutsiya zhivotnykh, Leningrad. pp. 46-47.
[*Littorina sitchana*, *L. kurila*, and *L. squalida* of the Pacific show the greatest tolerance for low salinity. They are close to the ancestral forms from which derived the Atlantic species, *L. saxatilis*, *L. obtusata*, and *L. littorea*. *Littorina mandshurica* and *L. brevicula* have a much lower osmotic tolerance. It is assumed the evolution of these two groups took place relatively independently.]
- BERGER, V. YA. & A. N. KUZ'MIN. 1978. The influence of lowered salinity on the development of some White Sea mollusks. ZZ 57(11):1632-1636(ES).
[Minimum normal salinities were found to be 17-18‰ for *Littorina obtusata* and 15‰ for *Littorina littorea*, *L. saxatilis*, *Ephera vineta* and *Margarites helicinus*; lower salinities halt development and ultimately destroy embryos and larvae.]
- GALKIN, YU. I. 1978. The influence of climatic variation on the distribution of archaeogastropods in the Barents Sea. Morfol. sistematika i evolyutsiya zhivotnykh. Leningrad. pp. 7-9.
- GALKIN, YU. I. & L. I. MOSKALEV. 1979. On the differences between 2 related species of prosobranch gastropods *Tectura virginea* (Muller, 1776) and *Problemacmea rubella* (Fabricius, 1780) (Gastropoda, Tecturidae). TZI 80:102-107.
[Differing in conchological features, mode of reproduction and geographic distribution, the species are most easily distinguished, despite their very similar radulae, by the presence or absence of a dark border along the inner aperture of the shell.]
- GUL'BIN, V. V. 1978. Prosobranch gastropods of the littoral of the northwestern part of the Sea of Japan. 2SC, pp. 30-31.
- GUL'BIN, V. V. 1978. The species and ecology of the Docoglossa of the Kurile Island shelf. SRF, no. 3, pp. 32-34.
[Vertical and substrate distribution as well as feeding and reproductive biology are examined.]
- GUL'BIN, V. V. 1979. A new gastropod species from the littoral of Far Eastern Seas. BMV, no. 3, pp. 88-89(ES).
[*Jeffreysina golikova* n. sp. (Rissoellidae) figured (radula and shell).]
- KARABELI, O. Z. 1978. Gastropods of the section *Eurycaspia* (genus *Turricaspia*, family Pyrgulidae) of the Caspian Sea. Dokl. MOIP. Zool. i botanika. Otd. Mosk. o-va. ispyt. prirodi. Moscow. pp. 30-32.
- LUKANIN, V. V. 1978. Peculiarities of the reaction of *Littorina* to various combinations of temperature and salinity. ZZ 57(9):1319-1323(ES).
[White Sea populations of *Littorina obtusata*, *L. littorea*, and *L. saxatilis* were studied and it was shown that temperature and salinity regimes uncharacteristic of the White Sea, even though they fell within the tolerance ranges of the species, were deleterious.]
- LUS, V. YA. 1978. A new abyssal buccinid species and some features of the morphology and anatomy of deep-water Pacific *Buccinum*. TIO 113:157-165(ES).
[*Buccinum crebricarinatum* from 3669 m in the Bering Sea is described, a maximum depth for buccinids. Anatomical remarks on other deep-water buccinids such as *Tacita* and *Calliloncha* compare these deep-water taxa with the sublittoral type-species *B. undatum* L.]
- LUS, V. YA. 1978. A new genus and species of Buccinidae from abyssal depths of the Idzu-Bonin Trench in the Pacific. TIO 113:147-156(ES).
[*Calliloncha solida* is described from the Idzu-Bonin Trench in depths of 6770-6850 m. Particulars of its shell, operculum, and gross anatomy are provided along with a discussion of buccinids in the abyssal and lower abyssal zone of the trenches of the Pacific Ocean.]
- MOSKALEV, L. J. 1978. Lepetellidae (Gastropoda, Prosobranchia) and related mollusks with similar shapes. TIO 113:132-146(ES).
[Lepetellidae Dall, 1882, Addisoniidae Dall, 1882, Cocculinellidae Moskaliev, 1971, and Bathyphytophilidae new family are examined. Their species composition and systematic placement among the pectinibranch gastropods are considered. The type-genus of the Bathyphytophilidae is the newly introduced, monotypic *Bathyphytophilus caribaeus* which inhabits depths of 2450-6780 m in the Caribbean region of the Atlantic Ocean and utilizes as food and substrate the rhizomes and possibly also the leaves of *Thalassia testudinum* which sink to abyssal and ultra-abyssal depths from shallow water. Another genus in this family is also newly introduced and monotypic: *Aenigmabonus kurilokamtschaticus* which lives in depths of 6120-8160 m.]
- MOSKVICHEVA, I. M. 1979. On the systematics of the Viviparidae of Far Eastern USSR. TZI 80:87-92.
[6 species of viviparids occur in the Amur River basin, 2 of which are described as new: *Cipangopaludina zejaensis* and *C. suifunensis*. The new genus *Amuropaludina* is established with *Paludina praerosa* Gerstfeldt, 1859, as type-species by original designation.]
- NAKHOMOV, A. N., E. V. KUZ'MIN & M. V. KRIVOBOKOV. 1978. An analysis of the isosyme esterase in the adaptation of *Littorina littorea* to a decrease of salinity in its surroundings. Morfol. sistematika i evolyutsiya zhivotnykh, Leningrad. pp. 73-75.
- SLAVOSHEVSKAYA, L. V. 1979. The organization, reproduction, and the systematic position of "*Thapsiella*" *plicosa* (Smith) (Rissooidea) from the Sea of Japan. TZI 80:93-101.
[A comparison of *Thapsiella plicosa* with both *Onoba semicostata* (the type-species) and *O. semistriata* shows that *plicosa* belongs to the Onobidae. It is assumed that *plicosa* is closer to the far eastern *Onoba* than to the Mediterranean *Thapsiella*. *Thapsiella* and the far eastern *Onoba* appear to be distinct in shell structure, a feature testifying to the heterogeneity of this group. Until a revision of this group is undertaken, it may be advisable to preserve *plicosa* provisionally as "*Thapsiella*."]]
- STADNICHENKO, A. P. 1978. Comparative characteristics of the albumen spectra of the embryonic capsules and hemolymph of the Viviparidae. Vestnik zoologii, no. 5, pp. 91-94.
[Electrophoretic analysis revealed 7 fractions in adults of *Viviparus coniectus* while capsule fluid showed a characteristic different albumen and absence of one of the adult fractions.]
- ZHARKOVA, I. S. 1978. On rudimentary eyes of the low-abyssal

- species *Tacita holoserica* (Prosobranchia, Buccinidae). TIO 113: 166-168(ES).
- [In *Tacita holoserica* from 6090-6135 m, as in many deep water gastropods, vision is reduced or lacking. Histological sections disclosed rudiments of eyes which are decidedly reduced, of small size, not deeply buried in connective tissue, and lack pigmentation.]
- ZHARKOVA, I. S. 1978. Reduction of the organs of sight in some representatives of the order Diotocardia (Gastropoda: Prosobranchia). ZZ 57(11):1637-1640(ES).
- [A positive correlation was documented between reduced vision as noted histologically and increased depth from the littoral to the ultra-abysal. Species investigated were the littoral patellid *Patella piperata*, the lepetids *Cryptobranchia concentrica* from 23 m and *Lepetella tubicola*, and the cocculinids *Tentaoculus perlucida* from 300-450 m, *Caymanabyssa spina* from 6740-6780 m, and *Fedikovella caymanensis* from 6800 m.]
- ### GASTROPODA, PULMONATA, AQUATIC
- GUNDRIZER, V. A. & YA. I. STAROBOGATOV. 1979. New species of freshwater mollusks of the Lower Yenisei basin. ZZ 58(8): 1130-1135(ES).
- [New members of *Lymnaea* (*Peregriana*) include *L. kurejkae* and *L. dolgini*, which form a special species group; *L. igarkae* belongs to the group of *L. ovata*, and *L. dipkunensis* to the group of *L. mucronata*. Diagnostic features of the shell and reproductive systems are delineated.]
- KRUGLOV, N. D. & G. V. BEREZKINA. 1978. Some questions on the physiology of reproduction in Lymnaeidae. NDVS 11:49-53. [Four different modes of copulation are described; additionally the role of the spermatheca in the absorption of surplus allosperm is documented.]
- LOGVINENKO, B. M., S. M. GERMAN & O. P. KODOLOVA. 1979. A study of the seasonal changes in the esterase system and shell morphology of *Lymnaea stagnalis*. ZZ 58(9):1307-1312(ES).
- [In populations of the pond snail, morphological features of the shell are more variable than certain characteristics, namely those of particular protein-enzyme relationships as determined electrophoretically.]
- POTAPINA, N. V. 1978. On the origin of the cells which form capsules around alien bodies in *Lymnaea stagnalis* L. Ontogenez 9(6):639-642(ES).
- [Autoradiographic analyses showed cells originating in the blood.]
- ZATRAVKIN, M. N. 1979. Variability of the common pond snail *Lymnaea stagnalis* from two natural populations. ZZ 58(8): 1230-1233(ES).
- [One population from shallow waters of the Bay of Bolshoye Miassova was contrasted to another from the Il'minsk River, both in the Il'minsk Preserve. The water in the bay partially dries up in summer and freezes to the bottom in winter; hence its snail population lives under very rigorous conditions. There is a distinct difference in the shells of the different populations and this difference was shown to be due to resistance to the effects of gamma rays at gastrulation: the bay form, which was shown to be more resistant, is characterized by smaller dimensions and a taller shell with a narrow aperture.]
- ### GASTROPODA, PULMONATA, TERRESTRIAL
- AL'MUKHAMBETOVA, S. K. 1979. New species of Pupilloidea (Mollusca; Gastropoda) from the Zailiisk Alatau. Izv. (Akad. Nauk) KazSSR. (News of the Acad. Sci. Kazakh SSR) Ser. Biol. (1979). No. 3, 30-33 (Kazakh Summary).
- [3 new species described.]
- ARUTYUNOVA, L. D. 1978. On the annual cycle of *Deroceras caucasicum* and *Vitrinoides monticola* (Limacidae) under laboratory conditions. Bio. zh. Armenii (Armenian Journal of Biology) 31(9):990-992.
- [Both species lived for 2 years on a diet of cabbage, carrots, and potatoes; *V. monticola* had 1 generation a year, and egg laying took place in 8.5-9.5 months, with time of incubation 1.5-3.5 months; the species overwinters in the egg stage. *Deroceras caucasicum* has 4 generations a year with egg laying beginning at the age of 2 months; incubation was up to 1 month.]
- DMITRIEVA, E. F. 1978. "Critical" periods in the ontogenesis of *Deroceras reticulatum* in connection with bio-climatic conditions of the Leningrad district. Nauch. tr. Leningr. s.-kh. inta (Scientific works of the Leningrad institute) 351:62-64.
- IVANOV, V. A. 1978. The slug fauna of the northern slopes of the Central Caucasus. Ekol. zhivotnykh sev. sklonov Tsent. Kavkaza (Ecology of animals from the northern slopes of Central Caucasus), Ordzhonikidze. pp. 92-94.
- [*Pseudomilax orientalis* and *Arion subfuscus* are newly recorded from the region.]
- KHOKHUTKIN, I. M. & A. I. LAZAREVA. 1978. Polymorphism in a population of terrestrial pulmonates. Fiziol. i populyatsion. ecol. zhivotnykh (Physiological and population ecology of animals), Saratov, no. 5/7, pp. 148-150.
- [In 1965 the populations of 8 species (over 20,000 samples) of Helicoidea, mainly *Bradybaena fruticum*, were examined: polymorphism appeared principally in shell coloration with 2 phenotypes.]
- KHOKHUTKIN, I. M. & A. I. LAZAREVA. 1979. Changes in growth and structure in a population of *Bradybaena*. Trudi Inst. Ekol. Rast. i Zhivotnikh. Uralsk. nauch. tsentra (Works of the Institute on the ecology and distribution of animals. Ural Scientific Center), Acad. Sci. USSR, no. 1, pp. 107-122.
- [*Bradybaena fruticum* and *B. lantzi* basically are annuals with few individuals surviving beyond one year.]
- KOVALEV, V. A. 1979. Responses of the statocysts of *Helix vulgaris* to vibrational stimulation. ZEBF 15:94-95.
- [Results demonstrated the ability of the statocyst to react to fluctuations of the substrate within a range of 30-1000 Hz.]
- LIKHAREV, I. M. & A. I. VIKTOR. 1979. Structural parallelisms and the systematic position of slugs in the suborder Stylomatophora. TZI 80:70-86.
- [Slug-like representatives of the superfamilies Arionoidea (Philomycidae, Arionidae), Zonotoidea (Parmacellidae, Milacidae) Limacoidea (Agriolimacidae, Limacidae and Boettgeriellidae) and Trionochochlamydoidea (Trionochochlamydidae) are discussed.]
- LIVSHITZ, G. M. & A. A. SHILEIKO. 1978. The life cycle of *Brephulopsis bidens*. Ekologiya 5:77-83.
- [Although the maximum life span is 2.5 years, not more than one-third of the population attains this age with the remainder dying by 1.5 years. The pre-reproductive age lasts about 1 year and mating occurs from April to May, with eggs being laid in May to June. The animals bury themselves a few centimeters in the soil to hibernate from November to March.]
- SHIKOV, E. V. 1979. The land snail fauna of populated areas of the Valdai Hills and adjacent territories. ZZ 58(7):966-976(ES).
- [The districts of Kalinin, Novgorod, Pskov, Moscow, and Leningrad were examined.]
- SHILEIKO, A. A. 1979. The systematics of the order Geophila (=Helicida) (Gastropoda, Pulmonata). TZI 80:44-69.
- [A new taxonomic scheme of the Geophila is proposed, based

upon an analysis of the methods and direction of the morphological development of characteristics of the shell, foot, and excretory and reproductive systems. The order is divided into 5 suborders: Achatinina new, Oleacinina new, Pupillina new, Helixina new, and Limaxina new. Within the suborder Helixina there are 3 infraorders: Endodontinia new, Helixinia new, and Zonitinia new. The infraorder Endodontinia is regarded as transitional to the 2 other infraorders. The Limaxina is divided into 2 infraorders: Trigonochlamydia new, and Limaxinia new. A discussion of the systematic position and phylogenetic relationship of the basic subordinate taxa is presented. It is shown that in the course of evolution the following lines of parallel and convergent specializations in the development of different organs and structures took place: (1) The establishment of sigmoidurethry entirely in the primitive and secondary urethra. (2) The formation of the aulacopod foot, at times accompanied by the beginning of a tripartite sole. (3) The reduction of the shell and the development of the slug-like form. (4) The transformation into predators.]

UVLIEVA, K. K. 1979. The agriculturally harmful slugs of south-east Kazakhstan. Alma-Ata, Nauka. 59 pp.

[Handbook designed for scientific workers, agronomists, and gardeners.]

VALIAKHMEDOV, B. & Z. IZZATULLAEV. 1979. On the distribution of terrestrial pulmonates in the soils of the vertical zone of Tadzhikistan. ZZ 58(6):810-815(ES).

[Distribution is determined by soil-climate conditions.]

ZEIFERT, D. V. 1978. Weight determination of terrestrial mollusks by morphometric indices. Probl. pochv. zool. Minsk. pp. 93-95.

ZEIFERT, D. V. 1978. Experimental measurement of respiration in terrestrial mollusks. Fauna, ekol. i izmenchivost' zhivotnykh (Fauna, ecology and variability of animals), Sverdlovsk. pp. 26-27.

GASTROPODA, OPISTHOBRANCHIA

ROGINSKAYA, T. S. 1978. The first deep-water capture and extension of range for *Coryphella stimpsoni* (Verrill) (Gastropoda, Nudibranchia). TIO 113:169-177(ES).

[Formerly this species was known only from the northwestern Atlantic Ocean and the White and Barents seas from the littoral to 200 m. Based on samples in the Zoological Institute in Leningrad, it was found that the species occurs, in addition to the Sea of Japan at depths to 3620 m, also in the Okhotsk, Kara, and Laptev seas. A map showing this distribution is provided and some aspects of the animal's reproductive biology are discussed.]

ZAITSEVA, O. V. 1978. Characteristics of the neuronal composition of the central nervous system of nudibranch mollusks. ZEBF 14(5):497-504.

[*Coryphella rufibranchialis*, *Dendronotus arborescens*, and *Cadlina laevis* of the White Sea were studied in various stages of post-larval development. The position of the largest neurons was mapped. For *C. rufibranchialis* and *D. arborescens* about 65-78 neurons were noted and a few of their characteristics described as well as age variations in body size, shape, pigmentation, and neurosecretory activity. With the help of impregnation with silver nitrate, 2 types of branching were discovered in the processes of several neurons.]

BIVALVIA

ALYAKRINSKAYA, I. O. 1979. Biochemical prerequisites for the survival of mussels. PDM, pp. 47-48.

[Optimum conditions obtain at weak alkalinity levels; with greater acidity, dissolution of the shell occurs. The muco-ciliary feeding mechanism is effective against polluted, even petroleum polluted, waters.]

AVEDEEVA-MARKOVSKAYA, E. B. 1978. On the structure of the settlement-mass of *Modiolus difficilis* (Kuroda and Habe). 2 SC, pp. 3-4.

[The most favorable substrate for attachment of *Modiolus* is sandy silt at 2-6 m. Here, masses are formed wherein the young attach themselves to dead and dying individuals and settled larvae are found among the hairy periostracum. In such a settlement, males are dominant but not significantly so, and sexually immature forms constitute 20-30% of individuals.]

DENISENKO, S. G. 1979. Duration of life and growth in the Iceland Scallop (*Chlamys islandica*) on the coasts of the Eastern Murmansk Peninsula. Biol. Probl. Severa 8th Simpoz. (8th Symposium of the biological problems in the north), Apatity, pp. 107-108.

DROZDOV, A. L. 1979. The ultrastructure of spermatids and spermatozooids of *Crenomytilus grayanus*. PDM, pp. 53-54.

DROZDOV, A. L. & V. A. KULIKOVA. 1979. The development of *Crenomytilus grayanus* Dunker. Observations on its life cycle. PDM, pp. 54-56.

[Discussed are the sizes of the eggs, stages of larval development, formation of prodissoconchs 1 and 2, and the settling of spat.]

DZYUBA, S. M. 1979. Oogenesis and the sexual cycle of *Crenomytilus grayanus* in Peter the Great Bay. PDM, pp. 50-52.

[Spawning takes place in May and August; developmental stages of gametogenesis in the intervening periods are described.]

FROLOVA, L. T. 1979. Seasonal changes in the intestinal epithelium of *Crenomytilus grayanus*. PDM, pp. 122-124.

[Cellular activity is lower during times of low temperatures in winter and early spring as a correlate of lowered levels of food; division processes increase during summer but then are reduced after spawning.]

GOROMOSOVA, S. A. & A. Z. SHAPIRO. 1978. Biochemical adaptations of energy exchange in mussels under different environmental conditions. 2SC, pp. 32-33.

GOROMOSOVA, S. A. & V. A. TAMOZHNYAYA. 1979. Transaminase activity in the tissues of the mussel (*Mytilus edulis*). Biol. morya (Kiev) 48:70-75(ES).

GOROMOSOVA, S. A. & A. Z. SHAPIRO. 1979. Changes in the activity of the synthesis of glycogen and fructose 1-6-diphosphatase in the tissues of *Mytilus galloprovincialis*; seasonal aspects and under hypoxic conditions. PDM, pp. 12-13.

IVANOVA, M. B. 1979. On the prevalence and distribution of *Mytilus edulis* L. in the littoral of the seas of Far Eastern USSR. PDM, pp. 58-60.

[Estimates of biomass are given for distinct areas in the north-eastern Pacific.]

IZZATULLAEV, Z. 1978. Species composition among large bivalves [Unionidae] in central Asia. Biol. osnovy ryb. kh-va vodoemov Sredi Azii i Kazakhstana (The biological basis of the fishing industry in the waters of Central Asia and Kazakhstan), Frunze, pp. 65-67.

KAFANOV, A. I. 1978. Temperature variability of linear growth and life duration in 6 species of the subfamily Clinocardiinae Kafanov 1975 (Mollusca, Cardiidae). ZZ 57(10):1480-1488(ES).

[Correlations of life span with growth and temperature adhere to the law of the optimum.]

KARTAVTSEV, YU. F. 1979. Biochemical methods for the deter-

- mination of the systematic placement of several mytilids from the Sea of Japan, and a population-genetic analysis of them. PDM, pp. 62-64.
- [The species studied were *Mytilus edulis*, *M. coruscus*, *Crenomytilus grayanus*, *Modiolus difficilis*, *Adula falcatoidea*, *Septifer keenae*, *Musculista senhousia* and (the Black Sea) *Mytilus galloprovincialis*; all are readily distinguished electrophoretically. *Mytilus* species are genetically closer than those of other genera and *Crenomytilus* is closest to *Mytilus*.]
- KAUFMAN, Z. S. 1978. Temperature dependence for the period of gamete maturation and spawning of *Crassostrea virginica* Gmelin. GZ 14(4):34-35(ES).
- KHRISTOFOROVA, N. K., N. I. BOGDANOVA & A. N. OBUKHOV. 1979. The contents of several metals in the soft tissues of *Tridacna squamosa* in the islands of the Pacific tropics, in connection with the environmental conditions. BMV, no. 3, pp. 67-73(ES).
- [Fe, Mn, Cu, Zn, and Pb concentrations in *Tridacna* correlated with the geochemistry of particular islands.]
- KOSENKO, L. A. 1979. An auto-radiographic study of the male sexual cells of the coastal scallop (*Patinopecten yessoensis*). BMV, no. 3, pp. 44-49(ES).
- [Nucleic acid synthesis was high in autumn and correlated with active reproduction of spermatogonia.]
- KRIVOSHEINA, L. V. 1978. Shallow water Pisidiidae (subfamily Euglesinae) of the upper Irtysh basin. ZZ 57(10):1489-1500(ES).
- [54 species were recognized, of which 10 are in the subfamily Sphaeriastriinae and 44 in Euglesinae, including 38 *Euglesa*, 5 *Neopisidium* and 1 *Odhneripisidium*; 10 are described as new. The distribution of these small bivalves is not as extensive as was previously assumed.]
- KRIVOSHEINA, L. V. 1979. New species of *Neopisidium* from eastern Kazakhstan. ZZ 58(4):602-605(ES).
- [5 species occur in the basin of the upper Irtysh, 2 of which are new: *Neopisidium altaicum* and *N. ovatotrigonum*.]
- KULIKOVA, V. A. 1978. The morphology, seasonal population dynamics, and settlement of the larvae of *Musculista senhousia* in Busse Lagoon [Aniwa Bay] (South Sakhalin). BMV, no. 4, pp. 61-66(ES).
- [Reproduction peaks during the warm summer months; the larvae, abundant components of the plankton, are pelagic for 15-20 days and their favored settling places are on the alga *Ahnfeltia* and *Sargassum* seaweed.]
- KULIKOVA, V. A. 1979. Characteristics of bivalve reproduction in Busse Lagoon, the Sea of Okhotsk, as affected by water temperatures. BMV, no. 5, pp. 34-38(ES).
- [Despite the peculiar temperature regime of this lagoon in south Sakhalin Island, the majority of bivalves found there have adjusted to a shorter pelagic larval period and spawn at maximum temperatures.]
- LOGVINENKO, B. M. & O. P. KODOLOVA. 1979. An electrophoretic comparison of species of Unionacea. Vestnik MGU biol. (Biological Herald of Moscow State University) 2:65-66(ES).
- [Six species of Unionidae (including *Anodonta* and *Unio*) and a single Margaritiferidae were contrasted by disk-electrophoresis.]
- LUKANIN, V. V. 1979. Cellular and organ-level reactions of White Sea *Mytilus edulis* to changes in salinity. ZOB 40(5):746-750(ES).
- [Adaptations to lowered salinity are modulated chiefly by the plasticity of tissues, which is presumably genotypically regulated; these include respiratory sensitivity and ctenidial stability.]
- MAKSIMOVICH, N. V. 1979. Some features of the reproductive cycle of *Mytilus edulis* in the Chupa Inlet [Kandalakshskaya Guba] (White Sea). PDM, pp. 84-86.
- [Animals mature sexually in 1-2 years and the sex ratio is near to 1:1; several developmental stages are delineated in gametogenesis; spawning takes place in July (10-17°C) with peaks of larvae in the plankton in July-August; settling is maximum in less than 5 m.]
- MANDRYKA, O. N. 1979. Features of the linear growth of *Patinopecten yessoensis* in populations of the Sea of Japan. BMV, no. 3, pp. 39-43(ES).
- [Five populations from various parts of the area were studied; differences of growth rate differed by area; maximum length (220 mm) was found in western areas and the length of life does not exceed 11 years.]
- MARGULIS, B. A., A. D. TARTAKOVSKII & G. P. PINAEV. 1978. The protein-contracting albumens of the molluscan adductor muscles. III. Electrophoretic methods of analysis for the extraction of actinomyosin and paramyosin. SFC, no. 3, pp. 71-75.
- MATVEEVA, T. A. 1979. Adaptations of egg bearing in some bivalve species. TZI 80:39-43.
- [Examples are given of various Arctic bivalves that brood their eggs and embryos to protect them from unfavorable external conditions.]
- MOTAVKIN, P. A., A. A. VARAKSIN & L. A. KOSENKO. 1978. Seasonal characteristics of spermatogenesis in *Crenomytilus grayana*. SRF, USSR, no. 3, pp. 58-61.
- [In June at the time of spawning, maximum maturity is attained.]
- NATOCHIN, YU. V., O. YU. MIKHAILOVA, E. A. LAVROVA & V. V. KHLEBOVICH. 1979. Water and electrolytes in the adductor muscles of *Mytilus edulis* during acclimatization to lower salinity *in vivo* and *in vitro*. ZEBF 15(4):419-425(ES).
- [Acclimatization of adductor cells to altered salinities is not modulated by neurohumoral influences.]
- NATOCHIN, YU. V., O. YU. MIKHAILOVA, E. A. LAVROVA & V. V. KHLEBOVICH. 1979. Water content and electrolytes in adductor muscles of *Mytilus edulis* in a wide range of salinities. BMV, no. 4, pp. 54-60(ES).
- [Muscle preparations exposed to different salinities showed correlative concentrations of sodium, potassium, and magnesium.]
- NIKIFOROV, S. M. 1979. On the systematics of oysters from the southern Primorye [province of far eastern USSR]. BMV, no. 5, pp. 25-33(ES).
- [Despite contentions of previous authors (RAZIN, 1934; HIRASE, 1930), who recognized 3 separate species (*gigas*, *laperousi* and *posjetica*), electrophoretic analyses show that only a single species, *Crassostrea gigas*, is present, supporting a view held by SKARLATO (1960).]
- PETROV, S. A. & A. YA. ROZANOV. 1979. The influence of functionally associated vitamins on the loss of 35S lipid acidity in Black Sea mussels from marine waters. Vzaimodeistvie mezhdru vodoi i zhiv. veschestvom. Trudi Mezhdunar. Simpoz. Odessa 1975. (Mutual interaction between water and living matter. Works of an International Symposium. Odessa). Vol. 2, Moscow, 1979, pp. 190-191.
- [The complex of vitamins basically increases the loss of lipids in ocean water.]
- PIPAEV, G. P. & S. YU. KHAITLINA. 1978. The protein-contracting albumen of the molluscan adductor muscles. I. Peculiarities of the adductor apparatus of freshwater mollusks and perspectives for its study. SRF, no. 3, pp. 62-65.
- [Structural and physiological peculiarities of various muscles are

determined by differences in the composition of minor protein-contracting albumens, which perform regulatory functions.]

PLISETSKAYA, E. M., L. B. SOLTITSKAYA & L. G. LEIBSON. 1979. The role of insulin in metabolic regulation in marine bivalves. *ZEBF* 15(3):288-294.

[Changes in carbohydrate metabolism develop more rapidly in mobile mollusks (*Pecten*) than in sedentary forms (*Mytilus*).]

SADKOV, A. N. & N. L. SEMENOVA. 1979. The biocenosis of *Portlandia arctica*-*Nuculana pernula* (Mollusca, Bivalvia) in Kandalaksh Bay, the White Sea. *ZZ* 58(6):797-803(ES).

[The community dominated by these two species (up to 60% of the total biomass which ranges from 10 to 60 g/m² extends to 120 m in depth.)]

SADYKHOVA, I. A. 1979. Biological characteristics of *Mya arenaria* in the White Sea. *ZZ* 58(6):804-809(ES).

[In Chupa Inlet of Kandalaksha Bay, most *Mya arenaria* reproduce in mid-July; young measure 0.3 to 0.5 mm in the last days of July. Salinities of less than 18‰ are not favorable for growth and individuals in the 3-5 year category predominate. Individuals measuring 70-79 mm are 8-10 years of age or more. Individuals 30-45 mm long or 3-4 years old are sexually mature. Siphons are often damaged by predatory sandpipers.]

SHAKHMAEV, N. K. 1979. The accumulation of manganese in *Anodonta anatina*. *ZZ* 58(6):919(ES).

[In mussels in the Miassa River, Chelyabinsk Prov., significant amounts of Mn were found in the foot, gonads, and gills where the concentration is highest at 7.15 mg/g.]

SHELUD'KO, N. S., S. YU. KHAITLINA & G. P. PINAEV. 1978. The protein-contracting albumens of the molluscan adductor apparatus. II. The albumen contents of myofibrils of 2 species of mollusks and of a rabbit. *SRF*, no. 3, pp. 66-70.

[*Patinopecten yessoensis* and *Mercenaria stimpsoni* were examined.]

SHELUD'KO, N. S., C. YU. KHAITLINA & G. P. PINAEV. 1978. The protein-contracting albumens of molluscan adductor muscles. IV. A study of the extraction of several protein-contracting albumens from the adductors of *Patinopecten yessoensis*. *SRF*, no. 3, pp. 76-80.

SKARLATO, O. A. 1979. Bivalves of economic importance and their role in the ecosystem. *Zool. Inst. Acad. Sci. USSR*, 131 pp., ill.

[Species of the genera *Mytilus*, *Crenomytilus*, and *Modiolus* were considered in regard to their distribution and population dynamics.]

SKARLATO, O. A. & YA. I. STAROBOGATOV. 1979. The systematic position and distribution of mussels. *PDM*, pp. 106-111.

[The following are treated: Subfamily Mytilinae, comprising 4 genera, *Crenomytilus* lives in the northern part of the Pacific; its single Recent representative, *C. grayanus grayanus*, is a Pacific Asiatic low boreal species found in subtropical waters. *Mytilus* embraces 2 subgenera, the nominative and *Crassimytilus*, n. gen., with type-species *M. coruscus*. This is a Pacific Asiatic subtropical species. The nominative subgenus includes 2 species: *M. edulis* has 4 subspecies, 2 of which are new. The range is amphiboreal; and *M. galloprovincialis* is an Atlantic and Mediterranean European low boreal subtropical species.]

SKARLATO, O. A. & YA. I. STAROBOGATOV. 1979. Basic features of the evolution and systematics of the Class Bivalvia. *TZI* 80: 5-38.

[The following stages can be seen in the evolution of the Bivalvia: (1) The formation of a monomyarian condition with a straight dorsal margin; (2) The formation of the Protobranchia; (3) The formation of the Autobranchia with their branchial filtering ap-

paratus and with a ciliated, water-moving mechanism; (4) The formation of the Septibranchia with a septal membranous pump; (5) The adaptive radiation of orders within the limits of the 3 named superorders. The evolution of the stomach and hinge and also the formation of the basic adaptive type of Bivalvia are discussed. Data on the systematics of the class, down to families, are given.]

SKUL'SKI, I. A., I. V. BUROVINA, N. B. PIVOVAROVA, T. I. IVANOVA & A. V. LANIN. 1979. Influence of environmental salinity on the ionic composition of hemolymph and tissue in mussels. *BMV*, no. 5, pp. 39-46(ES).

[Concentrations of Na⁺ and K⁺ were found to be, respectively, isotonic and hypertonic in samples of *Mytilus edulis*, *Crenomytilus grayanus*, and *M. galloprovincialis* from the Barents, Baltic, Black, and Japan seas.]

SOBETSKII, V. A. 1978. The conditions and perspectives of the study of late Cretaceous bivalves. *Dokl. MOIP. Zool. i botanika. Otd. Mosk. o-va. ispyt. prirodi. Moscow*. pp. 29-30.

SOBETSKII, V. A. 1979. The all-union symposium on morphology, systematics, phylogenesis, and ecogenesis of bivalves. *Tiraspol*, 3-4 Oct., 1978. *Paleontol. Zh.* 1:152-153.

STADNICHENKO, A. P. 1979. Some morphological regularities of growth in finger-nail clams (Sphaeriidae). *Vestnik Ekologii*, no. 2, pp. 27-32.

[Crimean samples showed correlations in measurements of shell length, height, and convexity.]

SULTANOV, K. M., S. A. ISAEV & K. F. OGLOBIN. 1978. Biogeochemical studies of iron in molluscan shells. *Okeanologiya* 18(6):1022-1027(ES).

[Iron content was examined in 230 Recent and fossil shells. The character of change of level of concentration in ontogeny was traced, as well as its dependence on ecological factors, the growth rate, and the organic contents of the skeleton. The main ways iron enters shells are discussed.]

SVESHNIKOV, V. A. 1979. The morphology of mytilid larvae. *PDM*, pp. 103-104.

[The larval shell and soft parts are described; these are in the water column ordinarily from June-September, and after settling the larval shell-shape is basically preserved into the adult stage.]

TUL'CHINSKAYA, V. P. & V. V. GUBANOV. 1979. A study of the bacterial contamination by intestinal bacilli and parahemolytic viruses. *PDM*, pp. 120-122.

USHEVA, L. N. & V. M. FAKTOR. 1978. A study of the DNA content in the intestinal epithelium of the yezo scallop. *BMV*, no. 4, pp. 81-84(ES).

[The nucleus of intestinal cells of *Patinopecten yessoensis* has a diploid quantity of DNA.]

USHEVA, L. N. 1979. Cellular structure of the epithelium of the digestive diverticulum in *Patinopecten yessoensis*. *BMV*, no. 4, pp. 61-67(ES).

[The cells are characterized histologically and autoradiographically.]

WIEGMAN, E. P. 1979. On growth rates in *Crenomytilus grayanus* (Cyrtodontida, Mytilidae) in Vostok Cove (Peter the Great Bay). *ZZ* 58(4):605-607(ES).

[On the average, mussels grow 12.4 mm the first year and 11 mm the second year; they become sexually mature at 60-70 mm.]

WIEGMAN, E. P. 1979. Survival of mussels in the aggregate masses of *Crenomytilus grayanus* (Cyrtodontida, Mytilidae). *ZZ* 58(3):306-313.

[Like many mytilids, *Crenomytilus grayanus* forms aggregate

masses of shells among which young settling mussels find a safer place for settlement.]

YAROSLAVSTEVA, L. M. & S. V. FEDOSEEVA. 1978. Adaptations of some marine mollusks to life in estuaries. BMV, no. 5, pp. 20–25(ES).

[*Nuttallia olivacea* and *Venerupis japonica* were studied in relation to the cellular mechanisms in adapting to lowered salinity; principal correlation to survival to decreased salinities was organismic, i.e., depth of burrowing.]

ZHUCHIKHINA, A. A. & I. A. SKUL'SKII. 1979. Characteristics of ionic potassium activation of muscular pyruvate kinase in mollusks living in various salinities. BMV, no. 2, pp. 82–86(ES).

[Using *Mytilus edulis*, *M. galloprovincialis*, *Crenomytilus grayanus*, and *Anodonta cygnea*, the authors show that the activation of pyruvate kinase by ionic potassium is higher in tissues of those inhabiting fresh, or lower salinity, water.]

ZOLOTAREV, V. N. & N. I. SELIN. 1979. The use of shell age-markings for the study of the growth rates in the mussel, *Crenomytilus grayanus*. BMV, no. 5, pp. 77–79(ES).

[Radioactive labelling showed that the invagination of the inner aragonitic layer into the outer calcitic layer takes place during the course of one year.]

ZOLOTAREV, V. N. 1978. On changes in the growth rate of marine mollusks. 2SC, pp. 41–42.

[Contrasts in the growth rates were studied in populations of *Crenomytilus grayanus* over the years 1855–1875 and 1920–1940.]

CEPHALOPODA

KORZUN, YU. V., K. N. NESIS, CH. M. NIGMATULLIN, A. A. OSTAPENKO & M. A. PINCHUKOV. 1979. New data on the distribution of the Ommastrephidae in the world ocean. Okeanologiya 19(4):707–711(ES).

[*Illex illecebrosus illecebrosus* was taken in the Mid-Atlantic Ridge (48°30'–56°N), *I. i. coindetti* from off Namibia (17°30'S), and the supposed bottom dwelling *I. i. argentinus* was captured on the surface above the continental slope and deep ocean. *Todaropsis eblanae* was found in the SW part of the Indian Ocean (Saya-de-Malha and Nazareth Banks of the Sea of Timor). *Todarodes angolensis* was taken near New Zealand, the Auckland and Campbell Islands, and SW and S of Tasmania. Other new data include: *Notodarus sloani* (possibly a subspecies) off southern Somalia and on the Saya-de-Mahla Bank; *Eucleoteuthis luminosa* in the SE part of the Indian Ocean and off the Norfolk Islands. *Todarodes sagittatus* is widely distributed over the Mid-Atlantic Ridge and on seamounts of the non-tropical North Atlantic, especially on the Kelvin and Corner Seamounts. For the southern form of *O. bartrami*, the part of its range in the Indian Ocean is isolated from the Pacific Ocean portion. Spawning swarms were observed near Idzu and Norfolk Islands.]

NESIS, K. N. 1978. *Nautilus* in aquaria. Priroda, no. 7, pp. 43–50.

[*Nautilus* grows and matures at depths of 100 or 200 to 500 m at 14–16°C, but reproduces in shallow reefs at 25–30°C. Mating

takes place from June to August or September and spawning a few weeks afterwards. Eggs are deposited singly at night; they are oval, 20–40 mm long by 15–35 mm in diameter, weigh about 3.5 g, and are encapsulated in a cartilaginous covering; 10–11 eggs are laid. Incubation apparently takes about half a year. Hatching takes place when the juveniles are about 2 cm in diameter. *Nautilus* is nocturnal and hides during the day in dark places or clings strongly to boulders with its tentacles. They move slowly. Buoyancy is regulated by changing the osmotic pressure in the cameral fluids. They feed on weakly moving or motionless prey. Vision is poor but they react strongly to sound and have a well developed chemotactile sense.]

NESIS, K. N. 1979. The larvae of Cephalopoda. BMV, no. 4, pp. 26–37(ES).

[All cephalopods do not have direct development; they may have a pelagic larval stage or a direct benthonic one. Postnatal ontogenesis may include various phases, i.e., from hatching to absorption of the internal yolk sac or from larval fry to subadult, sometimes accompanied with allometric growth of organs.]

NESIS, K. N. 1979. Larvae of the squid family Ommastrephidae. ZZ 58(1):17–30(ES).

[The larvae of 12 species and 8 genera are described and figured; generic determination is possible in the rhynchoteuthis stage but specific characteristics do not appear until later. Zuév's phylogenetic scheme is basically correct for the higher classification; however, *Ornithoteuthis* should be placed into separate subfamily while *Dosidiscus* is derived from the earliest common ommastrephid stock.]

NESIS, K. N. & CH. M. NIGMATULLIN. 1978. A discovery of an egg mass of the bottom octopus *Eledone caparti* (Octopodidae) in stomachs of deep-water blue sharks. ZZ 57(9):1324–1329(ES).

[From 250–380 km, off the coast of Dakar and Cabo Verde, Senegal, 3 blue sharks were taken by longline and their stomachs contained undigested egg masses of 2800–5100 eggs of, presumably, *Eledone caparti*; the embryos were at stage XIII; eggs at early developmental stages measure 8.9 × 3.8 mm, slightly larger than those of *E. cirrosa*.]

NESIS, K. N. & CH. M. NIGMATULLIN. 1979. Distribution and biology of *Ornithoteuthis* Okada, 1927 and *Hyaloteuthis* Gray, 1849 (Oegopsida). Byul. Mosk. o-va. ispit. prirodi, Otd. Biol. 84(1):50–63(ES). (Bull. of the Moscow Naturalists Society, Series Biology).

[From plankton hauls and fish stomachs, the authors showed the geographic and vertical distribution, size at sexual maturity, and other ecological data for *Ornithoteuthis antillarum*, *O. volatilis*, and *Hyaloteuthis pelagica*; species of *Ornithoteuthis* were tropical nerito-oceanic, actively attacked by predators, and smaller at maturity.]

SHEVTSOVA, S. V., A. P. BESTKIN, K. N. NESIS & E. V. ROZENGART. 1979. Divergences in the properties of cholinesterases in the visual ganglia of *Ommastrephes bartrami* (Les.): squids as an index of the isolation of populations in various parts of a discontinuous range. Okeanologiya 19(3):481–486(ES).

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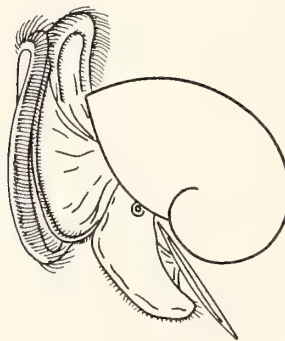
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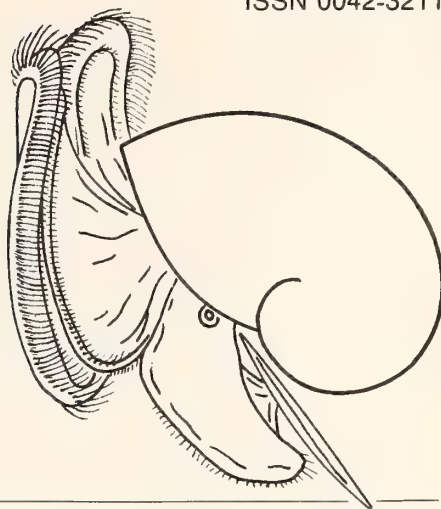
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Adaptive Value of Shell Variation in *Thais lamellosa*: Effect of Thick Shells on Vulnerability to and Preference by Crabs

by

A. RICHARD PALMER

Department of Zoology, University of Alberta, Edmonton, Alberta T6G 2E9 and
Bamfield Marine Station, Bamfield, British Columbia V0R 1B0, Canada

Abstract. Laboratory experiments with the predatory shallow-water crab *Cancer productus* revealed that thin-shelled individuals of the morphologically variable prosobranch gastropod *Thais lamellosa* (Gmelin, 1791) (= *Nucella lamellosa*; Muricacea; Thaididae) were significantly more likely to be eaten than thicker shelled individuals. Three of five crabs of different sizes (8.0–16.5 cm carapace width) were able to eat the largest thin-shelled snail offered (>45 mm shell length) over a period of 55 days. However, only the largest crab ate more than 10% of the thick-shelled snails offered over this same time period, and it was also able to eat the largest thick-shelled snail available (44.6 mm); hence, thick shells did not guarantee immunity from predation. Significantly, the few snails eaten from the “thick-shelled” population by the remaining four smaller crabs averaged nearly two standard deviations (mean = 1.99) lighter than the mean for animals of comparable length from that population, revealing that individuals further from the mean were selected against. The time sequence of consumption suggested that motivational state strongly influenced whether a crab attacked thick-shelled snails successfully: for all but one crab, thick-shelled snails were not consumed until more than 50% of the thin-shelled individuals had been eaten.

The adaptive value of thick shells appears to result from two factors: (1) a decrease in the range of sizes of crabs to which a snail of a given body size is ultimately vulnerable, and (2) a decrease in the desirability of snails to the larger crabs to which they are still vulnerable. Variation in shell thickness probably persists in *Thais lamellosa*, however, because thinner shells are favored in the absence of crabs: they are less expensive to produce and to transport, and they permit more rapid growth when food is abundant.

INTRODUCTION

THE SHELLS OF *Thais lamellosa* (= *Nucella lamellosa*) are among the most variable of those of prosobranch gastropods from the Pacific coast of North America; they vary extensively in color, banding, sculpture, thickness, and shape (ABBOTT, 1974; KINCAID, 1957; KITCHING, 1976; SPIGHT, 1973, 1976). The variation in shell sculpture and thickness is perhaps the most dramatic; it is often correlated with habitat, and the mean phenotype of populations can change dramatically over distances as short as a few hundred meters (Palmer, unpublished). The adaptive value of shell variation in this species, however, has not been addressed experimentally. Because increased shell thick-

ness in *T. lamellosa* is often associated with habitats in which crabs, in particular *Cancer productus*, are abundant, I examined the effectiveness of thick shells as deterrents to this shell-breaking predator (ZIPSER & VERMEIJ, 1978). In addition, because larger crabs generally are capable of eating larger gastropods (VERMEIJ, 1978), I examined the relationship between crab size and relative vulnerability of thin- versus thick-shelled snails.

METHODS

Thais lamellosa of two substantially different shell morphologies (comparable to illustrations 1905 and 1908 of ABBOTT, 1974) were collected in early February from two

Table 1

Offered sizes, eaten sizes, and "critical sizes" (defined in text) at the termination of the experiment, of thin- and thick-shelled *Thais lamellosa* for each of the five *Cancer productus* used in the experiments. Crab sizes are carapace widths. Twenty-one snails were offered initially in each group, eaten snails were not replaced. Question marks following critical sizes indicate unrepresentative values because many smaller snails were available but not eaten.

		<i>Thais lamellosa</i> shell length (mm)					Final “critical size” (mm)
Crab size (cm)	Shell form	Offered		Eaten			
		Small- est	Larg- est	Small- est	Larg- est	n	
8.0	Thin	23.5	46.9	23.5	39.3	18	42.9
	Thick	20.1	46.2	22.8	22.8	1	24.0?
9.1	Thin	21.0	45.5	21.0	45.5	21	>45.5
	Thick	21.4	42.4	29.4	29.4	1	29.5?
9.2	Thin	21.3	48.0	21.3	48.0	21	>48.0
	Thick	20.2	46.0	20.0	46.0	2	>46.0?
13.5	Thin	21.8	52.8	21.8	52.4	20	52.6
	Thick	19.5	50.7	—	—	0	<19.5
16.5	Thin	22.7	54.8	22.7	54.8	21	>54.8
	Thick	21.5	44.6	21.5	44.6	20	>44.6

different habitats on San Juan Island, Washington (USA). Thin-shelled, strongly sculptured individuals were collected at low tide from an isolated, offshore rock surrounded by deep water and swept by strong tidal currents (Turn Rock, 48°32'N, 122°58'W), and thick-shelled, smooth individuals were collected from rocky substrata in quiet water surrounded by a muddy bottom near the east shore inside the mouth of False Bay (48°29'N, 123°04'W). The snails were numbered individually (PALMER, 1980), and measured for shell length (apex to tip of siphonal canal) to 0.1 mm with vernier calipers. To estimate shell weight, live animals were immersed in seawater, and immersed weights were converted to shell dry weights using the regression: shell dry weight (g) = 1.572 immersed weight (g) + 0.0162 ($r^2 = 0.9998$; from PALMER, 1982). To measure the body size of the animals (excluding the shell), tissue wet weight was also estimated for a subsample from each population by subtracting estimated shell weight from the whole weight of the animals in air (PALMER, 1982).

Five specimens of *Cancer productus* of different sizes (8.0–16.5 cm carapace width) were collected, from False Bay, during nighttime low tides over several weeks prior to the experiments. Each specimen was placed individually into shallow concrete seawater trays (30 × 50 × 15 cm) supplied with running seawater at the Friday Harbor Laboratories, Friday Harbor, Washington (USA). These trays were adjacent to a south-facing window, and no

attempt was made to regulate lighting conditions. I did not attempt to standardize hunger levels of the crabs prior to the experiments, but over the duration of the experiments the only food available to the crabs was the introduced snails. Water temperatures ranged from 6.5 to 7.7°C.

The experiments were initiated by introducing simultaneously into each aquarium 21 snails of a comparable size range for each shell type (Table 1). The behavior of the crabs was observed closely over the first five and one-half hours to evaluate their initial responses to the snails; these observations were not continued on subsequent days because feeding activity was too unpredictable. Snails crawling up the sides of the aquaria were knocked back onto the bottom daily for the first two weeks, and every two to four days for the remainder of the experiment to ensure their availability to the crabs. Both dislodged and attached snails were equally likely to be attacked by a crab. The snails remaining in each aquarium were noted nine times over the next 55 days (Feb. 12–April 3). Following each enumeration, the bottoms of the aquaria were siphon-vacuumed to collect all shell fragments, and the fragments were examined for the presence of numbered tags to verify that missing snails had in fact been eaten. Of the 210 snails used in these experiments, only one disappeared without being eaten, and one died from other causes; these were not included in the analyses.

Regression lines were compared using analysis of covariance (ANCOVA), and differences among expected means were compared using the appropriate standard errors (SOKAL & ROHLF, 1981).

RESULTS

Differences in shell weight between the two populations of *Thais lamellosa* were highly significant: for animals of the same shell length, those from False Bay ranged from 50 to 100% heavier with increasing size (shell weight for the False Bay population was significantly higher for all positive shell lengths [$P < 0.001$, comparison of predicted mean weights from shell length for both populations]), and larger animals had proportionally heavier shells (the slope for the thick-shelled population was significantly higher than that for the thin-shelled one [$P < 0.001$, ANCOVA; Figure 1a]). For both populations, the slopes were significantly less than 3.0 ($P < 0.001$; Figure 1a), revealing a negative allometry in each. Rather curiously, in spite of the differences in shell weight, the tissue weights of animals of the same shell length did not differ between the two populations ($P > 0.45$; Figure 1b); hence, the body size of animals from both populations could be predicted from the same regression on shell length. Geometrically, this means that the shells of individuals from the thick-shelled population were wider for a given length.

Initial feeding activity varied rather markedly among crabs. During five and one-half hours of continuous observation on the first day of the experiment, two of the crabs (8.0 and 16.5 cm carapace width) did not even at-

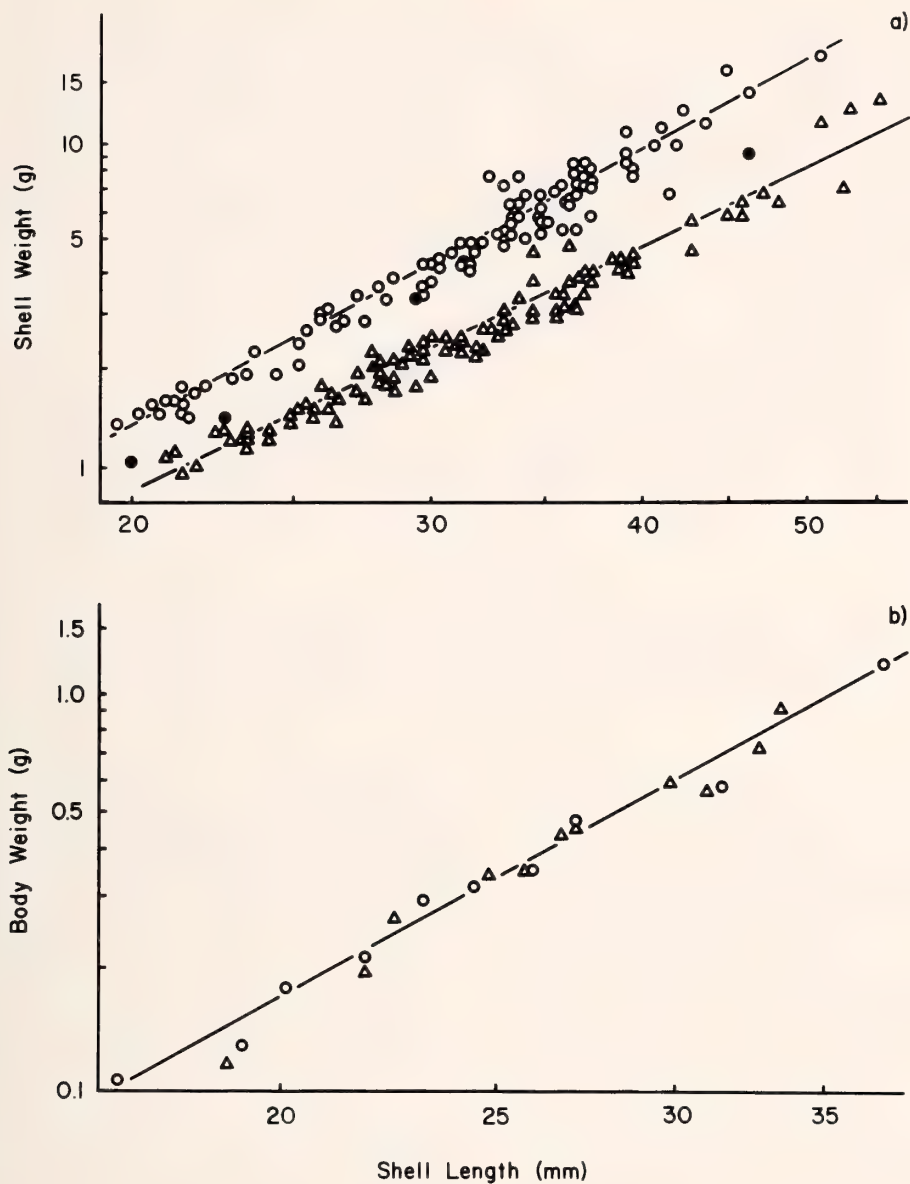


Figure 1

The relationships with shell length of shell weight (a) and body wet weight (b) for a thick- (circles) and a thin-shelled (triangles) population of *Thais lamellosa*. Solid circles in (a) indicate individuals eventually consumed by the smaller four crabs (see text). In (a), the regressions (\pm SE) of log shell weight (Y) on log shell length (X) for the two populations were: thick-shelled population, $Y = 2.787(\pm 0.060)X - 3.5030(\pm 0.006)$, $N = 106$, $r^2 = 0.953$; thin-shelled population, $Y = 2.450(\pm 0.050)X - 3.2588(\pm 0.005)$, $N = 106$, $r^2 = 0.958$. These slopes were significantly different ($P < 0.001$, ANCOVA). In (b) $\log(\text{body wet weight}) = 3.1904(\pm 0.105)\log(\text{shell length}) - 4.9279(\pm 0.009)$ (both populations combined; neither the slopes nor the adjusted means from ANCOVA were significantly different between populations [$P = 0.45$ and $P = 0.79$ respectively]).

tempt to eat any snails and one (13.5 cm) only investigated two thick-shelled snails but did not attempt to break their shells. A fourth crab (9.2 cm) attacked two thin- and three thick-shelled snails; it consumed one, and badly damaged the shell of the other thin-shelled individual, but it was unable to inflict any damage on the three thick-shelled

animals. In contrast, the fifth crab (9.1 cm) attacked and consumed five thin-shelled snails, and attacked two thick-shelled individuals unsuccessfully.

Differences in feeding behavior among crabs persisted for the first two weeks of the experiment (Figure 2). Within eight days of the start of the experiments, three of the five

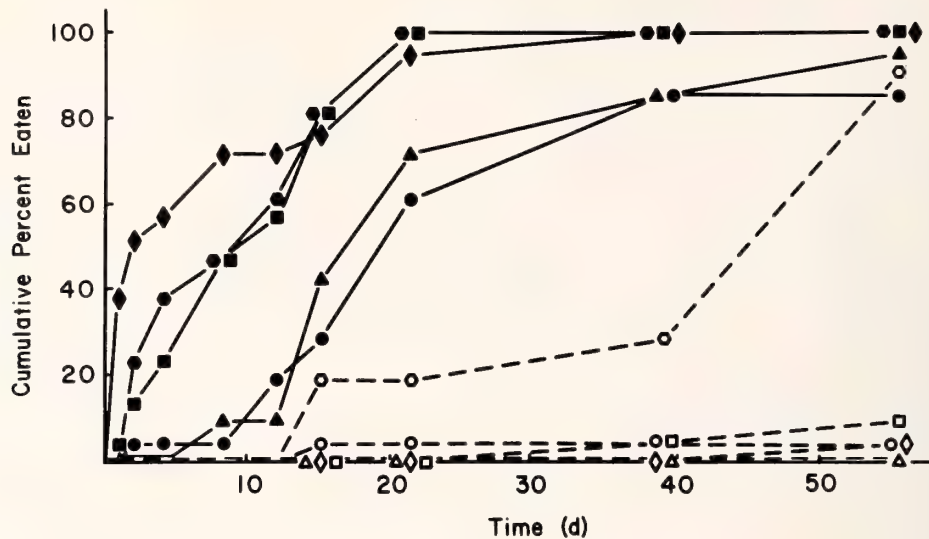


Figure 2

Cumulative percent of thick- and thin-shelled *Thais lamellosa* consumed as a function of time by each of five crabs. Solid symbols with solid lines: snails from the thin-shelled population. Open symbols with dashed lines: snails from the thick-shelled population. Different symbols correspond to crabs of different carapace widths: circles, 8.0 cm; diamonds, 9.1 cm; squares, 9.2 cm; triangles, 13.5 cm; hexagons, 16.5 cm.

specimens of *Cancer productus* had eaten nearly 50% of the thin-shelled *Thais lamellosa*. The remaining two did not consume that many of the thin-shelled form until after two weeks had elapsed.

In spite of the variation in feeding behavior among crabs,

snails of the two different shell types were consumed at significantly different rates (Figure 2; thin = 0.36 snails/day, thick = 0.09 snails/day; $P = 0.025$, Mann-Whitney U-test). Only the largest crab (16.5 cm carapace width) ate many of the thick-shelled form; after 55 days it had

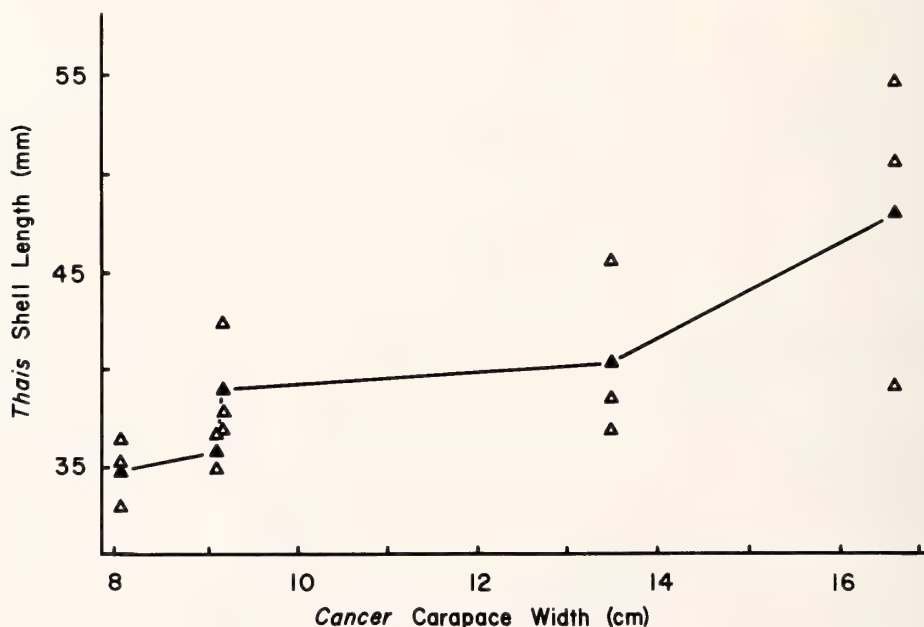


Figure 3

Shell lengths of the largest three thin-shelled *Thais lamellosa* eaten at LD 50 as a function of *Cancer productus* size (carapace width). Open symbols, individual snails; solid symbols, mean. $N = 15$, $r^2 = 0.609$, $P < 0.01$.

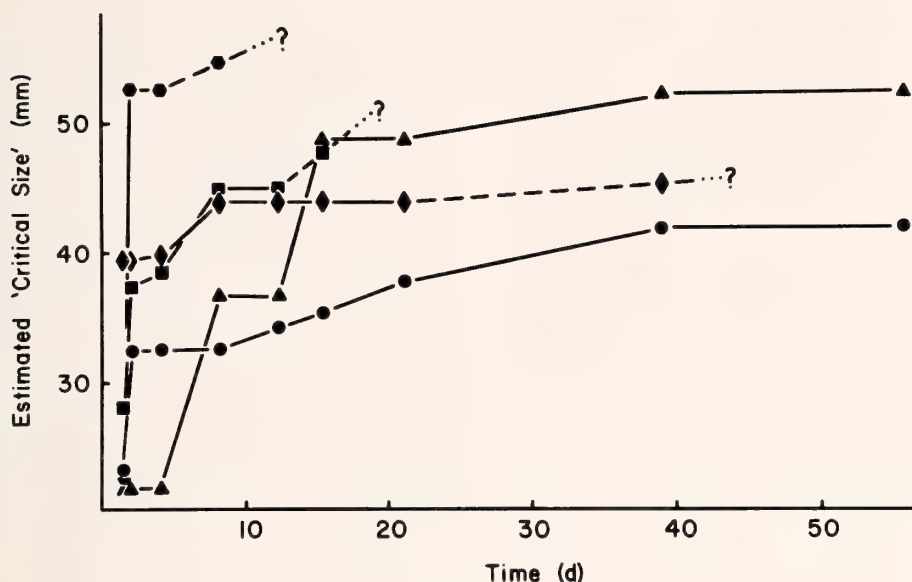


Figure 4

Change in the estimated "critical size" (mean shell length of the largest snail eaten and the next largest available; VERMEIJ, 1976) for each of the five crabs over the duration of the experiment. Dashed lines indicate that the largest available snail had been consumed during that interval; thus the estimated critical size would probably have continued to increase. Symbols for the crabs as in Figure 2.

consumed all but one of the initial 21 thick-shelled snails, in addition to all of the thin-shelled ones. The remaining four crabs ate at most only two of the 21 available thick-shelled snails even though three of them had eaten all, or all but one, of the thin-shelled snails. In addition, only one of these four crabs ate a thick-shelled snail before 50% of the thin-shelled snails had been eaten in its aquarium (Figure 2), and it was the only thick-shelled snail eaten by this crab. Thus, many thin-shelled snails were eaten before the crabs began attacking thick-shelled ones successfully.

Finally, the sizes of the largest thin-shelled snails eaten increased with crab size after 50% of those available had been consumed (Figure 3), even though, by the end of the experiment, three of the five crabs had eaten all of the thin-shelled snails available. Thus, smaller thin-shelled snails tended to be eaten before larger ones, particularly for the smaller crabs (see also Figure 4 below). For the two crabs that did not eat all of the thin-shelled snails, the final "critical size" (mean of shell length of the largest snail eaten and the next largest available; VERMEIJ, 1976) increased with crab size (Table 1). Final critical size was not related to crab size for the thick-shelled snails (Table 1), because the few snails eaten by the four smaller crabs were among the lightest of the thick-shelled animals offered, averaging 1.99 SD less than their expected values from regression (Figure 1a); thus, these values overestimate the actual critical sizes for the thick-shelled population.

DISCUSSION

Thaidid gastropods are notorious for their variation in shell appearance, variation that has been a frequent source of taxonomic confusion (ABBOTT, 1974; GRANT & GALE, 1931; KINCAID, 1957, 1964; VOKES, 1971; WELLINGTON & KURIS, 1983). The conspicuousness of this variation has resulted in many descriptive studies of geographic patterns within members of this family, including patterns in shell color (BERRY & CROTHERS, 1968, 1974; MOORE, 1936; SPIGHT, 1976) and in shell morphology (CROTHERS, 1982, and references therein; CURREY & HUGHES, 1982; KINCAID, 1957, 1964; KITCHING, 1976, 1977; PHILLIPS *et al.*, 1973; SEED, 1978; VERMEIJ & CURREY, 1980). A few studies have examined experimentally the potential adaptive value of morphological variation in these species (EBLING *et al.*, 1964; HUGHES & ELNER, 1979; KITCHING & LOCKWOOD, 1974; KITCHING *et al.*, 1966; WELLINGTON & KURIS, 1983), and they all have demonstrated, among other things, that thicker shelled individuals are more resistant to attack by shell-breaking crabs than thinner shelled ones. The results presented here support the conclusions of these experimental studies; however, they also demonstrate that thicker shells cannot guarantee immunity from predation by large crabs, and they reveal a probable additional advantage to thicker shells that relates to the motivational state of crabs.

The laboratory feeding experiments with *Cancer productus* yielded three results of significance. First, thicker

(=heavier) shelled individuals of *Thais lamellosa* were consumed at a much lower rate than thinner (=lighter) shelled ones by all sizes of crabs. Second, the largest *C. productus* was nonetheless capable of eventually consuming all sizes of the thicker shelled snails offered (up to 44.6 mm). Third, the successful attack of thicker shelled or larger snails was influenced by the availability of thinner shelled or smaller animals.

I use shell weight as interchangeable with shell thickness because of the convenience with which it can be measured and because I feel it is a more useful single measure of average thickness. Local increases in thickness associated with axial sculpture or apertural teeth make thickness measurements of a specific part of the shell arbitrary and sometimes difficult to interpret. Apertural teeth and axial sculpture may thicken the lip, reducing vulnerability to crabs that peel shells starting at the aperture, but such shells would still be vulnerable to crabs that crush (VERMEIJ, 1978). *Cancer productus* uses both techniques (ZIPSER & VERMEIJ, 1978); thus, shell weight provides a measure of average shell thickness that is more likely to reflect relative vulnerability of snails to this crab.

The adaptive value of thick shells appears to be a consequence of two factors. First, thicker shells decrease the size range of crabs to which snails of a given body size are ultimately vulnerable (see also REIMCHEN, 1982). The four smaller crabs in the experiments ate at most two of the available thicker shelled morph of *Thais lamellosa*, and all of these eaten snails had the thinnest shells of those available of comparable length (Figure 1a). Thus, sufficiently thick shells can render their bearers invulnerable to attack from all but very large crabs. This in turn reduces the total number of crabs to which the snails are potentially vulnerable and hence reduces their overall probability of mortality.

A second advantage to thicker shells results from the selective feeding behavior of crabs. When a diversity of prey is available, predators usually feed preferentially on the energetically more valuable prey (HUGHES, 1980; HUGHES & ELNER, 1979; PALMER, 1984). By increasing both the energy expended and the time required to break open a shell successfully, thicker shells will decrease the potential food value of snails to shell-breaking predators. This decrease in potential food value probably accounts for an aspect of the feeding behavior exhibited by all but one of the crabs that consumed one or more thick-shelled *Thais lamellosa*: the thick-shelled snails were not attacked successfully until more than 50% of the thin-shelled ones had been eaten (Figure 2). For the largest crab, which ate nearly all of the thick-shelled snails offered, 80% of the thick-shelled individuals were eaten only after all of the thin-shelled snails had been consumed (Figure 2). Had thinner shelled snails been replaced as they were eaten, the remaining 80% of the thick-shelled animals probably would not have been eaten. These results suggest strongly that thicker shelled snails were manipulated but rejected as undesirable by crabs earlier in the experiments.

Similarly, at 50% mortality of the thin-shelled snails, the mean size of the largest snails eaten increased with crab size ($r^2 = 0.61$; Figure 3), presumably reflecting an increase in the "preferred size" for the larger crabs when thin-shelled snails were initially abundant (ELNER & HUGHES, 1978). However, by the end of the experiments, the largest four crabs had eaten all, or all but one, of the thin-shelled *Thais lamellosa*. Hence, although larger snails were ultimately vulnerable, they were not consumed until most of the smaller ones had been eaten, again suggesting they were manipulated and rejected earlier in the experiment. Access to alternative prey of higher food value (energy/unit time, or potential for promoting growth; PALMER, 1983a) thus appears to influence substantially the probability of being eaten of more heavily defended or larger prey that are nonetheless still potentially vulnerable to crabs. A similar conclusion has been reached by BOULDING (1984) from experiments with *Cancer productus* feeding on infaunal bivalves.

In these experiments, the increase over time in the maximum size of snail eaten by individual crabs points to a methodological difficulty associated with measuring the "critical size" of different shell forms (maximum size of vulnerability to a given size and species of shell-breaking predator [VERMEIJ, 1976]—a larger critical size means snails are vulnerable to a larger size, i.e., are more vulnerable). Clearly, the estimated critical size (mean size of the largest individual eaten and the next largest one available) depends upon the duration of the experiment (Figure 4). It will also depend upon the availability of alternative prey. When a number of prey are offered simultaneously to a predator, curves such as those of Figure 4 will increase confidence in the accuracy of the experimentally measured critical sizes (see also BOULDING, 1984), particularly for crabs, whose feeding activity in the lab is often erratic and unpredictable.

Finally, if thicker shells significantly reduce vulnerability to shell-breaking predators, why are not all populations of *Thais lamellosa* in particular, or all species of marine gastropods in general, thick-shelled? Presumably, the costs of a thicker shell outweigh the advantages in some cases. Shell material, or at least the organic matrix of shells, appears to be energetically expensive to produce (PALMER, 1983b, and references therein). Heavier shells are also more expensive to transport in surface-dwelling species; a two-fold increase in shell weight results in nearly a three-fold increase in the cost of locomotion in *T. lamellosa* (Palmer and LaBarbera, in preparation). In addition, the maximum rate of body growth in *T. lamellosa* is limited by the rate at which shell material can be produced rather than by the rate of ingestion or rate of tissue production (PALMER, 1981); thus, a thicker shelled individual would not be able to grow as rapidly as a thinner shelled one even when food is not limiting. All of these costs will counteract the selection for thicker shells as mortality due to shell-breaking predators decreases. The shell-thickness polymorphism in *Thais lamellosa* probably per-

sists because genetic fixation is prevented by some combination of (1) gene flow among adjacent populations subject to different intensities of predation, and (2) temporal fluctuations in crab abundance, which favor different phenotypes at different times at a given site.

Uncertainty exists over the degree of genetic control of intraspecific variation in shell morphology of thaidid gastropods. Because the variation among populations is usually greater than that within, it is often assumed to be genetic (CROTHERS, 1974, 1982; KINCAID, 1957; KITCHING & LOCKWOOD, 1974). However, the same pattern would result if this morphological variation were purely phenotypic. Growth in the laboratory of young individuals collected from populations of different adult morphology suggests that considerable phenotypic plasticity exists in the shell sculpture of *Nucella lapillus* (LARGEN, 1971) and shell shape of *Thais lamellosa* (SPIGHT, 1973). Breeding studies with *T. emarginata* have revealed that variation in spiral shell sculpture has both a genetic and an environmental basis (PALMER, 1985). Of the shell features that vary in both *T. emarginata* and *T. lamellosa*, shell thickness appears to be the most phenotypically labile (Palmer, unpublished), suggesting provocatively that these gastropods may be capable of producing predator-resistant shells in direct response to potential predation by crabs, as described for rotifers (GILBERT, 1966), bryozoans (YOSHIOKA, 1982; HARVELL, 1984), and cladocerans (GRANT & BAYLY, 1981) in response to their predators. Preliminary results (Appleton & Palmer, unpublished) have revealed that both thin- and thick-shelled *T. lamellosa* can be induced to produce thicker apertural lips in the presence of *Cancer productus* being fed conspecific snails.

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Gastropod Feeding Tracks as a Source of Data in Analysis of the Functional Morphology of Radulae

by

CAROLE S. HICKMAN

Department of Paleontology, University of California, Berkeley, California 94720

AND

TOM E. MORRIS

Department of Life Sciences, Fullerton College, Fullerton, California 92634

Abstract. Feeding tracks produced by the radulae of gastropods are potentially rich sources of data that (1) can help explain behavior and behavioral variation, (2) provide dietary evidence of the size, quantity, and specific nature of material that is removed and ingested, and (3) provide detailed evidence of the ways that natural biological materials fail when grazed.

Analysis of feeding tracks of the intertidal trochid *Tegula funebris* (A. Adams, 1854) on artificial substrates provides standard or idealized sets of impressions of feeding strokes for comparison with sets of impressions of actual interactions of teeth with materials in the normal diet of the species. *Tegula funebris* feeds in different ways on different substrates by varying the pressure applied to the radula, with results that vary from deep incisions to light brush marks. Different teeth contact the substrate during different feeding behaviors, and various forms of asymmetry are common features of feeding tracks. Feeding tracks can be characterized morphologically on three levels: (1) description of the static pattern of the track, (2) correlation of the incisions with the teeth that produced them, and (3) dynamic specification of the order in which individual incisions and groups of incisions are produced relative to the morphology and movements of the apparatus. The most accurate level of documentation requires frame-by-frame analysis of filmed feeding sequences of living animals.

INTRODUCTION

MOVEMENT AND FUNCTION of radular teeth and the nature of their interactions with food items and substrates are among the least well understood aspects of gastropod feeding. Function cannot be inferred from tooth form alone (HICKMAN, 1980) or even from correlations of tooth form and gut contents (HICKMAN, 1981b). In an earlier paper (MORRIS & HICKMAN, 1981) we emphasized the importance of configuration changes in the cylindrical radula of *Tegula funebris* (A. Adams, 1854) in producing a complex sequence of tooth movements during protraction and retraction. The purpose of this paper is to document the results of the basic feeding stroke of this rhipidoglossan

trochid gastropod on both artificial and natural substrates and to show how the stroke can be modified behaviorally to produce different results. Demonstration that *T. funebris* can use its radula to feed in different ways on different substrates argues for caution in interpreting correlations between tooth morphology and diet. On the other hand, a wealth of detailed information is available in radula-marred substrates and prey items, and we hope to stimulate interest in the morphology of feeding tracks as a source of functional inference.

Correlations between tooth form and diet are most common in specialized feeders. Some of the best documentations in marine gastropods are for *Conus* (NYBAKKEN, 1970)

and "grazing" carnivorous nudibranchs (McDONALD & NYBAKKEN, 1978; NYBAKKEN & McDONALD, 1981). However, the specific nature of radular damage to prey or interaction with the prey is not understood.

Characterizations of radula-damaged substrates are rare in the literature. Attention to substrate morphology has focused primarily on specialized systems, such as the morphology of boreholes produced by active predatory marine prosobranchs (CARRIKER, 1961, 1977; RADWIN & WELLS, 1968), or characteristic damage to foraminiferal tests produced by *Olivella* (HICKMAN & LIPPS, 1983). Surfaces of grazed substrates are the least well known but potentially rich sources of functional data. The potential is particularly well illustrated by STENECK, who has figured grazing incisions in crustose coralline algae at the level of cellular resolution (1982, fig. 5c; 1983, fig. 2) and estimated the number of epithelial cells consumed per bite by an acmaeid limpet (1982:512). However, as in the accounts of a correlative morphological nature, details of function are not understood relative to the incisions.

From a sedimentological viewpoint, there has been some interest in bioerosive damage to calcium carbonate substrates as a by-product of molluscan grazing. Some chitons and acmaeid limpets excavate shells to feed on boring algae (GOLUBIC *et al.*, 1975; FARROW & CLOKIE (1979). The importance of this process is emphasized by FARROW & CLOKIE (1979) who conclude that molluscan feeding is a major factor in recycling of carbonate from shells and in producing carbonate mud in a shallow seaway in Scotland.

From the perspective of geologic time, molluscan feeding traces on carbonate substrates have been reported as far back as the Upper Jurassic (BOEKSCHOTEN, 1967; VOIGT, 1977). At least some of these fossil grazing traces seem to be associated with algal-bored substrates (TAYLOR, 1981; AKPAN *et al.*, 1982). Because many of the fossil traces are closely similar in morphology to modern traces associated with chitons and acmaeid limpets, functional and behavioral interpretations should be possible once the modern traces have been analyzed correctly in functional terms.

Feeding track morphology has been studied most extensively by European biologists on aquarium walls or algal-coated plates (*Algen-platten*) (HUBENDICK, 1957; ANKEL, 1938; EIGENBRODT, 1941) and on glass surfaces coated with wax (*Fettplatten*) (MÄRKEL, 1957, 1966). It is these studies that inspired us to elaborate and extend the approach to a comparison of artificial surfaces with natural surfaces and items in the diet of *Tegula funebris*.

MATERIALS AND METHODS

To obtain a baseline description of the *idealized* feeding track (*i.e.*, tooth impressions produced by a single feeding stroke), it is necessary to have a flat, smooth, fine-grained surface that will retain three-dimensional impressions. It also must be a material to which snails are willing to

apply the radula. Experimentation with a variety of waxes and preparation techniques led to a procedure using beeswax (MORRIS, 1980).

To produce a smooth, shiny surface, melted (60°C) paper-filtered unpurified beeswax (Bee, Inc.) was poured 4 mm thick on cellophane stretched over 2.5-cm high aluminum rings supported by upside-down petri dish tops. After cooling to room temperature, individual beeswax disks were placed in a freezer for 1 h to harden. Rapid peeling of the cellophane membrane from the frozen wax produced a shiny surface.

Tegula funebris would not graze on new disks, but feeding tracks were readily obtained on disks that had been "cured" for one week in aerated natural seawater at 7°C. Individual snails were restricted to separate cured disks in finger bowls covered with porous polyethylene covers, so that feeding tracks could be correlated with specific radulae.

After washing grazed disks in distilled water, a great deal of information can be obtained by examining feeding tracks on dry disk surfaces with a dissecting microscope and low-angle reflected light. The illustrations in this paper were obtained with scanning electron microscopy from portions of disks removed with a hot scalpel, mounted on SEM stubs, and coated with gold palladium. Scanning electron microscopy permits resolution of individual tooth excavations at higher magnifications than are obtainable with a light microscope.

To obtain comparable observations of the effect of the feeding stroke on irregular surfaces and natural textures of the food items in the diet of *Tegula funebris*, individuals were allowed to graze in covered finger bowls on three algal species. *Laminaria dentigera*, *Iridaea splendens*, and the sporophytic rock-encrusting form of *Gigartina* sp. (formerly referred to *Petrocelis* sp.) were chosen to cover a range of variation in surface texture and topography. *Tegula funebris* has been observed feeding (making the behavioral motions that indicate protraction and retraction of the radula) on all three species in the field, as well as on a variety of other algae (authors' personal observations); and BEST (1964) concluded from experimental studies that, although *T. funebris* prefers fleshy macroalgae, it feeds on a variety of encrusting species as well.

Sections of algae with feeding tracks were cut out and fixed in 2.5% glutaraldehyde, postfixed in 1% osmium tetroxide, dehydrated through an ethanol series from 50% to 100%, and critical point dried. Dried specimens were coated with gold palladium and viewed over the same range of magnifications as the traces on the beeswax surfaces.

RESULTS

Feeding Tracks on Beeswax

Idealized tracks: Typical tracks of *Tegula funebris* on beeswax surfaces are illustrated in Figures 1-8. Each track is the result of a single feeding stroke or cycle of radular

protraction and retraction. During the feeding stroke the radula behaves as a flat band anteriorly and a slit cylinder posteriorly, with a movable semicircular crease at the region of transition that is controlled by the underlying odontophore. The configuration of the radula at maximum protraction is illustrated in Figure 9, and the cylindrical mode of function is outlined by MORRIS & HICKMAN (1981).

Each trace has two parts and is roughly bilaterally symmetrical. In a typical trace the two opposing incised regions are produced exclusively by marginal teeth and are separated by an untouched central region (Figures 1, 2). Although the rachidian and lateral teeth are the largest teeth in the radula, they are recessed between the tips of the odontophore and do not normally contact flat substrates during the feeding stroke.

The most prominent portions of the trace are the curved incisions of the individual innermost marginal teeth. Three or four rows of teeth are involved in the production of each trace. The sequence of movements is not intuitively obvious from the morphology of the apparatus, and the description of trace production is derived from frame-by-frame analysis of feeding strokes filmed through a microscope on plexiglass surfaces.

Traces in Figures 1–7 are all oriented with anterior at the top. Note that anterior and posterior correspond to the positions of the anterior (dorsal) and posterior (ventral) lips of the mouth as it is applied to the substratum. Thus the anterior end of each trace represents the leading edge of the direction of locomotion of the snail. In this usage, anterior and posterior on the trace do not correspond to anterior and posterior on the radula itself. Because the radula operates as a slit cylinder (MORRIS & HICKMAN, 1981), anterior and posterior rows of teeth are arranged concentrically, so that posterior is in the center and anterior is at the periphery (Figure 9). As a consequence of this configuration, the anterior end of each trace is made by the posterior rows of teeth and the posterior end of each trace by the anterior tooth rows.

The dominant mark in each trace is the single long and deep incision of the innermost marginal (Figures 1–4). Adjacent and anterior to the dominant incision is a series of successively shorter and shallower traces of the remaining five or six inner marginal teeth of the same row (Figures 1–4). This unit is repeated three to five times by the rows of inner marginal teeth that contact the substrate during the feeding stroke.

Figure 10a shows the relative positions and configuration of three marginal tooth rows at the beginning of the feeding stroke and the travel paths of the inner marginal teeth. From this diagram it should be clear why the posteriormost row strikes the substrate first to form the anteriormost unit of the trace; why the sequence of substrate contact within a row is from outer to inner marginals; and, finally, why the innermost dominant incision is the posteriormost incision in each unit on the substrate.

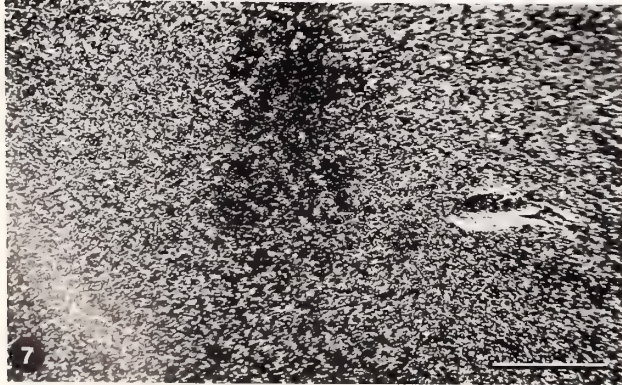
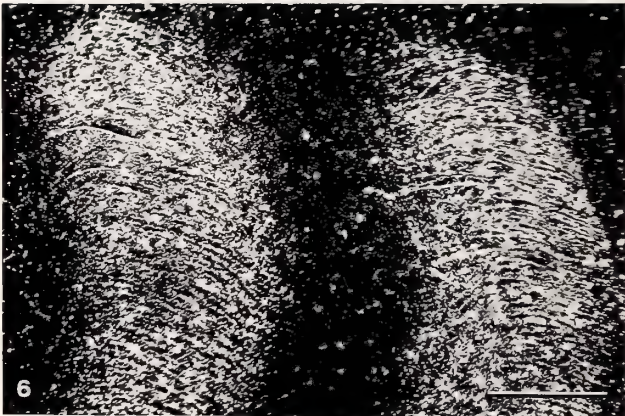
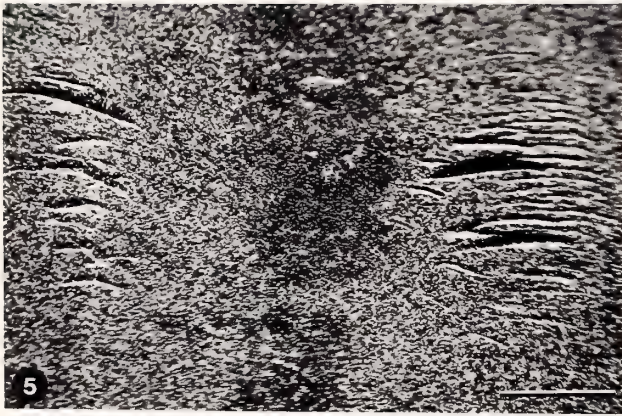
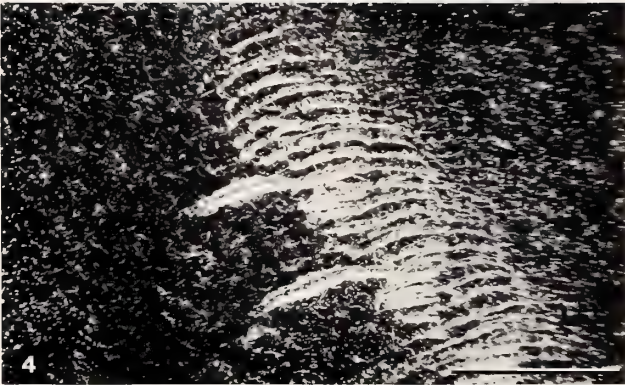
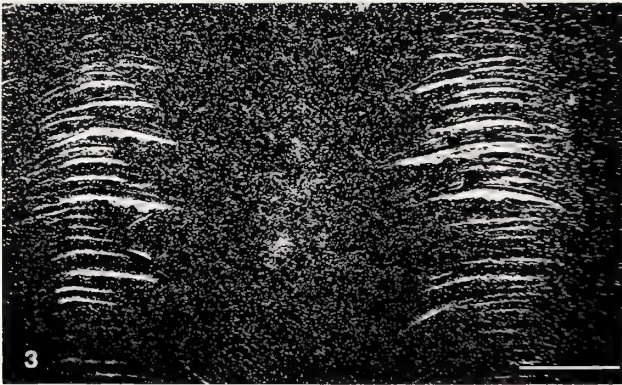
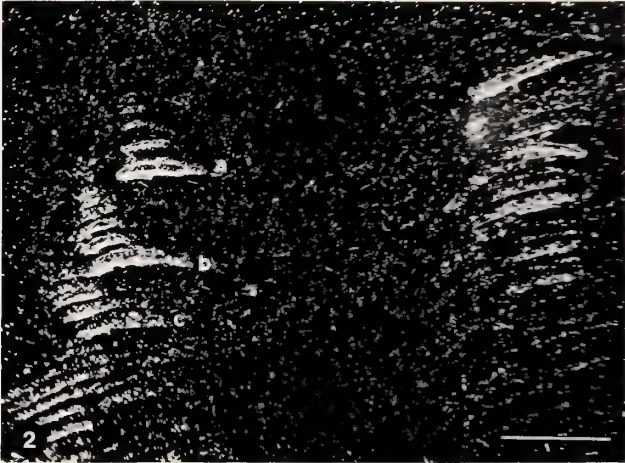
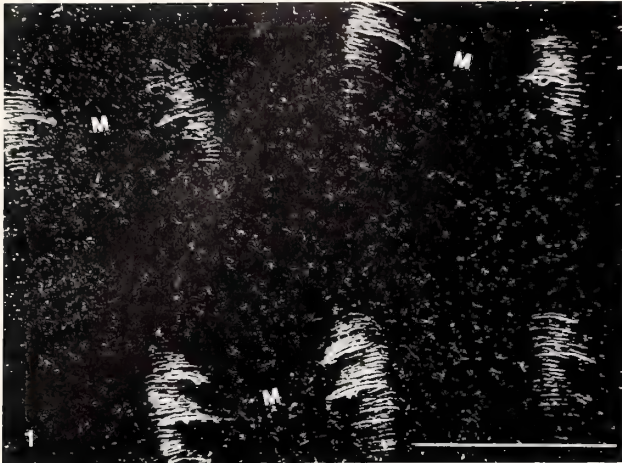
The path followed by a single row of teeth during the

feeding stroke is illustrated diagrammatically in Figure 10b. Only those portions of the row that pass directly over the odontophore and make substrate contact are illustrated. The heavy lines are successive tracings of the position of the row in sampled frames from 0 to 40 in one filmed feeding stroke. Zero represents maximum protraction and 40 represents the point at which the row leaves the substrate. Another way to view the same sequence is to follow the paths of individual teeth or groups of teeth. Figure 10c diagrams the paths of different major blocks of marginal teeth. Movement is toward the central axis of the diagram. On such a diagram, we can trace the path of any individual tooth from the point of initial contact to the point of lifting from the substrate. These two diagrams together further help explain why the sequence of contact of teeth in any given row is from outer to inner marginals and why the trace records the sequence in an anterior to posterior direction.

One final set of principles will be helpful in understanding the production of the trace. First, it is the inner marginals that move most directly over the tips of the two horns of the odontophore as substrate contact is made. Second, rates of travel vary for different sections of a single row, and the inner marginals act quickly, in a rapid “snapping” of the teeth as they flip over the cartilage at the inner edge of the *knickstelle* or semicircular crease. Third, facilitation of inner marginal “snapping” is furthered by the movement of the crease itself as the odontophore is drawn posteriorly during the feeding stroke. Fourth, the pointed cusps are rotating as they gouge the substrate to produce U-shaped incisions. Figure 8 is a low-angle micrograph showing the profiles and relative depths of incisions.

Variations: In contrast to the typical feeding track described above, some feeding tracks are dominated by fine brush marks of the mid and outer marginal teeth. Unlike the inner marginals, mid and outer marginal cusps do not make separate incisions. The upper surfaces of the cusps act in close concert as they are pressed against a flat substrate and drawn over it. The feeding stroke can be varied so that only brush marks are produced. Figure 5 shows a trace with both incisions and brush marks, while Figures 6 and 7 show traces that are dominated by mid and outer marginal brush marks.

A number of other variations appear in feeding tracks on the beeswax substrates. The number of rows that contact the substrate is variable (*i.e.*, the number of times that the basic unit is repeated from anterior to posterior). Furthermore, the number can vary from one side of the trace to the other, disrupting the bilateral symmetry (Figure 2). This kind of variation occurs because the right and left tips of the odontophore act independently and do not necessarily exert the same pressure on the right and left sides of the radula. Asymmetric traces can be produced in other ways, some of which are related to underlying patterns of asymmetry in the morphology itself (HICKMAN, 1981a,



1984), although behavioral asymmetries are more conspicuous in feeding tracks. For example, if the tips of the odontophore do not move synchronously (*i.e.*, if one is applied to the substrate in advance of the other) a trace may be produced in which one half will lie anterior to, or offset from, the other half (Figures 2, 6). Finally, if the tips of the odontophore do not move straight back (*i.e.*, parallel to the plane of symmetry of the idealized trace, the radula, and the head/foot), a curved trace will be produced. Figure 6 is a trace that was produced by odontophore tips both moving in parallel arcs. These are the most common forms of variation, although others occur, and they can be interpreted from what we know about tooth morphology, our knowledge of radular function, and by comparison with the idealized trace.

Feeding Tracks on Natural Substrates

In nature, *Tegula funebris* does not graze on beeswax or plexiglass, nor is it likely to encounter other surfaces that are perfectly flat and homogeneous. Examination of feeding tracks on algal surfaces confirms that the radula is used differently on different food items in the natural diet of the snails (Figures 11–14).

On the relatively flat blades of the brown alga *Laminaria dentigera* (Figures 11, 12) animals may leave paired sets of inner marginal incisions similar to those of the idealized feeding tracks on beeswax. As on the beeswax, the depth of incision is variable, and the tracks are frequently asymmetric. This type of incision was observed to release copious cell contents, which are preserved dried in Figure 11. In this form of feeding, no algal tissue is removed by the radula.

It would be tempting to conclude that *Tegula funebris* feeds on cell sap of *Laminaria*. However, animals also produce much deeper paired excavations on algal blades. Figure 13 shows an excavated feeding track from which

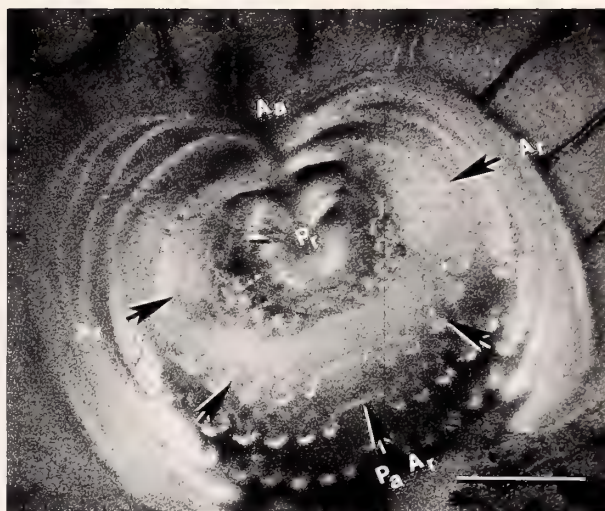


Figure 9

Optical micrograph of living *Tegula funebris* with radula protracted, from 35-mm negative. Note subcylindrical configuration with concentrically arrayed tooth rows. Anterior rows on the radula (A_r) are on the outside, while posterior rows (P_r) are in the center. A_a denotes anterior lip of the animal; A_p denotes posterior. Arrows show direction of row movement during retraction. Bar = 0.5 mm.

a significant volume of algal tissue has been removed. It does not seem possible that a single feeding stroke could have produced all this damage to the laminarian blade, and this may represent a series of feeding strokes "in place."

On the irregular blade surfaces of the red alga *Iridaea splendens*, feeding traces indicate yet another mode of feeding. Figure 14 shows a surface that has been brushed free of its attached microbiota with no sign of damage to the underlying blade. This light brushing of the surface by

Explanation of Figures 1 to 8

Scanning electron micrographs of feeding tracks of *Tegula funebris* on cured beeswax surfaces. Figures 1–7 are oriented with anterior ends of traces up. Note that in this orientation the order of trace formation is from top to bottom, with posterior rows striking the surface first.

Figure 1. Low magnification view of three separate traces, each produced by a single feeding stroke; M = the center of each trace. Bar = 1 mm.

Figure 2. Asymmetric feeding track produced by a single feeding stroke in which the left side is farther anterior and more disorganized due to independent behavior of the two tips of the odontophore. a, b, c = incisions of the innermost marginal teeth of three successive rows. Compare with Figure 10a for orientation. Bar = 400 μ m.

Figure 3. Single feeding track made by inner marginal teeth. Bar = 400 μ m.

Figure 4. Left half of an asymmetric feeding track with relatively deep inner marginal incisions. Note that at least 11 inner marginal teeth in the posteriormost row (anterior or top on the trace) contacted the substrate. Bar = 400 μ m.

Figure 5. Feeding track showing both inner marginal incisions and mid and outer marginal brush marks. Bar = 400 μ m.

Figure 6. Strongly asymmetric feeding track consisting of mid and outer marginal brush marks. Bar = 400 μ m.

Figure 7. Bilaterally symmetric feeding track consisting of light mid and outer marginal brush marks. Bar = 400 μ m.

Figure 8. Low-angle side view of left half of feeding track showing incisions of inner marginal teeth. Longest and deepest incisions are those of the innermost marginal; anterior is at right; individual tooth movement was from top to bottom; and sequence of incisions is from right and to left. Bar = 100 μ m.

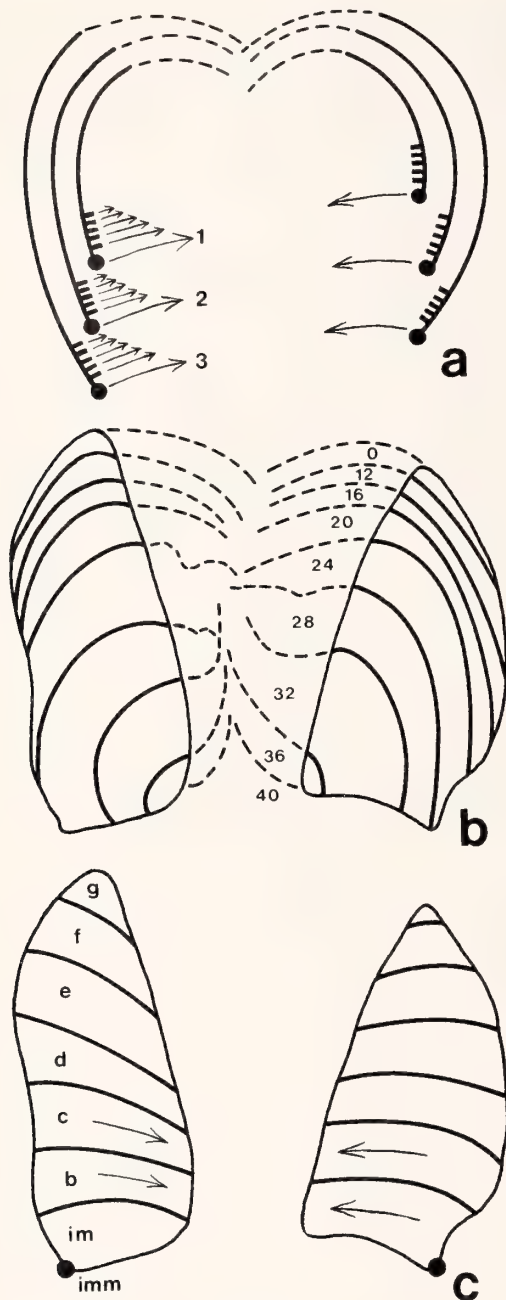


Figure 10

Dynamics of feeding track production, illustrated from analysis of 16-mm slow motion (64 frames/sec) film of *Tegula funebris* on wall of plexiglass aquarium. a. Position of three rows at beginning of feeding stroke (compare with Figure 9). Arrows show paths of marginal teeth (dominant inner marginal is represented by large dot); Row 1 (posteriormost on radula) passes over odontophore and strikes substrate first, followed by rows 2 and 3 (anterior on radula). Solid lines are portions of rows that make substrate contact. b. Diagram of successive tracings of the position of a single row over 40 frames in one filmed feeding stroke. Solid lines show row in contact with substrate; broken lines show position of retracted portions of rows no longer in

mid and outer marginal teeth is achieved through lessening the pressure applied to the radula by the odontophoral cartilage and is comparable to the type of brush track recorded on beeswax in Figures 6 and 7. This mode of feeding was also observed in snails feeding on the surface of the crustose sporophytic form of *Gigartina* spp. (formerly referred to as *Petrocelis franciscana*).

DISCUSSION AND CONCLUSIONS

Feeding tracks can be "described" on three levels. The morphology of the trace can be characterized most simply as a pattern of marks on the substrate. It also can be characterized by attributing individual marks to individual teeth or groups of teeth (a correlation of one static pattern with another). It can be characterized further at a dynamic level, as a temporal sequence that specifies the order in which individual marks and groups of marks are made relative to the complex ordering of movements of the radula and odontophore.

The first-order pattern can be described without reference to its production. The description, however, need not lack detail: a first-order description at high magnification of the ways that cell walls or the underlying biological materials have failed may contain a great deal of information. The second order of complexity requires knowledge of the morphology (and perhaps composition and structure) of the objects that contact the substrate to produce the trace. And the third order of complexity requires knowledge of how the morphology moves and works.

The methods and results outlined above provide a guide to description and analysis at each of the three levels. They also provide a direct approach to integrated understanding of radular functional morphology incorporating substrate data. It is not clear why so little attention has been paid to substrate data. Perhaps it is the combination of the microscopic scale of most feeding traces, their inconspicuousness, and the difficulty of observing, preserving, and collecting them in the field along with the individual animals that produced them.

To ignore substrate data, however, is analogous to attempting to analyze what a pencil is used for and how it functions by examining the pencil and watching someone manipulating it without ever examining how it is applied to a piece of paper or what appears on the paper. The marks on the paper are, in this instance, a particularly rich source of information about the functional possibilities of a pencil.

The approach that we advocate can be taken much further than we have taken it here. For example it can be

contact. c. Diagram of paths of movement of major blocks of teeth in a single row over the same 40-frame sequence depicted in B. imm = innermost marginal tooth; im = inner marginal tooth block (teeth producing incisions), and b-g = mid to outer marginal blocks.



Explanation of Figures 11 to 14

Scanning electron micrographs of surfaces of macroalgae after grazing by *Tegula funebris*.

Figure 11. Flat surface of *Laminaria dentigera* with inner marginal incisions and dried cell contents (at posterior end of each half of the feeding track). Bar = 400 μm .

Figure 12. *Laminaria dentigera* with single, lightly incised feeding trace. Bar = 400 μm .

Figure 13. *Laminaria dentigera* with paired deep excavations and algal tissue removed, probably the result of multiple feeding strokes in place. Bar = 400 μm .

Figure 14. Topographically irregular surface of *Iridaea splendens* with ungrazed microbiota on right and surface brushed free of epibionts on left. Bar = 40 μm .

extended to include consideration of the biomechanical properties of radulae and substrates and their interactions. LITTLER & LITTLER (1980) and STENECK & WATLING (1982) have suggested that both algae and algal grazers can be arrayed in "functional groups" related to estimated "toughness" of the alga and estimated "excavating abilities" of the feeding apparatus. Comparative study of radular morphology, methods of application of radulae to substrates, and feeding tracks point to major biomechanical difficulties with these predictions. Toughness may be an important property of *some* algae relative to *some* of the tools that *some* gastropods apply in *some* of their feeding behaviors. For other gastropods, other biomechanical properties of radular teeth and other biomechanical prop-

erties of substrates than toughness may be important. This is suggested by the radular morphology and composition, the method of function, and the substrates upon which some docoglossan limpets feed. Figure 15 illustrates the feeding tracks of *Collisella asmi* (Middendorff, 1847) incised in the calcium carbonate shell of its host, *Tegula funebris*. The significant properties of the mineral substrate are its brittleness and hardness relative to the brittleness and hardness of the heavily mineralized radular teeth. The significant feature of the manner in which this radula is drawn across the substrate and the linear grooves that result (Figure 15) is the abrasive mode of removal of material (which occurs in the gut in finely divided form). Note that the incisions in Figure 15 are produced parallel

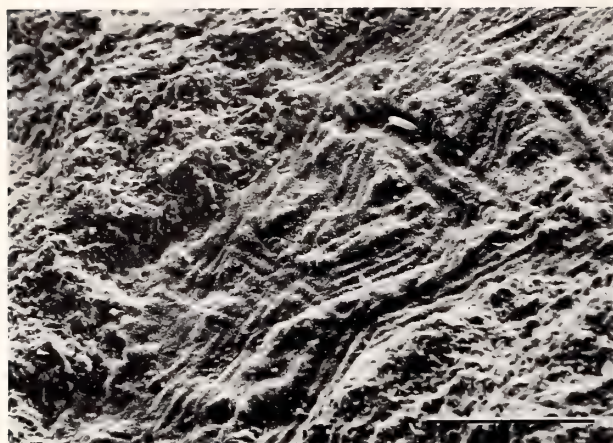


Figure 15

Feeding tracks of *Collisella asmi* incised in the shell of *Tegula funebris*. Each individual feeding stroke consists of four parallel grooves produced by abrasion from two inner lateral and two outer lateral tooth positions. Bar = 100 μ m.

to the longitudinal axis of the radular ribbon, in contrast to the incisions of the radula of *T. funebris*, which are normal to the axis. Wear patterns of individual docoglossan teeth are related to this abrasive mode of feeding (RUNHAM & THORNTON, 1967; KERTH, 1983) and, contrary to most wear patterns, the teeth maintain a sharp, efficient edge by virtue of use (HICKMAN, 1980).

Aside from applicability to functional morphological analysis and its biomechanical extensions, feeding track data can provide better documentation of gastropod feeding biology. Tabulations of dietary preferences of gastropods (see STENECK & WATLING, 1982, appendix 1 and references therein) are based primarily on observed substrate associations and gut contents. Feeding tracks provide more reliable and visually compelling estimates of what animals have actually taken from the substrate—liquid cell contents, tissue, surface epiphytes, etc. First-order observations are adequate for dietary documentation.

A final extension of feeding track analysis is into experimental ecology and tests of feeding theory. Substrates can be used experimentally to document and compare patterns of coverage and coverage efficiency, to produce estimates of materials removed per unit time, and to examine patterns of substrate use and partitioning in both single and multi-species systems.

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Predation by *Nucella cingulata* (Linnaeus, 1771) on Mussels, Particularly *Aulacomya ater* (Molina, 1782)

by

PATTI A. WICKENS AND CHARLES L. GRIFFITHS

Zoology Department, University of Cape Town, Rondebosch 7700, South Africa

Abstract. The whelk *Nucella cingulata* (Linnaeus, 1771) is abundant in the rocky intertidal zone of Marcus Island, South Africa, where it feeds on the mussels *Aulacomya ater* (Molina, 1782), *Choromytilus meridionalis* (Krauss, 1848), and *Perna perna* (Linnaeus, 1758). *Aulacomya ater* appears to be the preferred prey. The distribution of boreholes drilled in mussel shells collected from the field appears to be random, but borehole diameter is an increasing function of prey shell length. Laboratory feeding experiments confirm that larger individuals of *N. cingulata* drill wider boreholes and preferentially select bigger mussels. The energy value of food consumed increases rapidly with predator size, but this is accomplished by taking progressively larger prey rather than more of them. The overall impact of *N. cingulata* on the *A. ater* population is estimated and compared with that of other invertebrate predators. Although many small mussels are taken by predators, this often acts merely to reduce the intense intraspecific competition for space to which juvenile mussels are frequently subjected.

INTRODUCTION

Nucella cingulata (Linnaeus, 1771) is a predatory whelk that lives in the intertidal and subtidal zones of rocky shores along the west coast of southern Africa. Its principal prey items are the three species of mussel that occur in the area, namely the ribbed mussel *Aulacomya ater* (Molina, 1782), the black mussel *Choromytilus meridionalis* (Krauss, 1848), and the brown mussel *Perna perna* (Linnaeus, 1758). *Nucella cingulata* attacks its prey by drilling a hole through the shell, using alternating mechanical and chemical processes, i.e., rasping with the proboscis and secretion of acid by an accessory boring organ respectively, as described in related species by FRETTER & GRAHAM (1962). The flesh is subsequently extracted through the hole using the proboscis and consumed.

Predators utilizing this technique spend most of their time manipulating and ingesting prey and little in search and capture. BAYNE & SCULLARD (1978), for example, found that *Nucella lapillus* spent between 63 and 97 hours drilling and ingesting each prey item, and CONNELL (1970) discovered that *Thais* spp. spent approximately 70-80% of their feeding time in the process of drilling alone. Larger mussels naturally yield a greater amount of flesh and therefore more energy to the predator, but they also have thicker shells and therefore require a greater investment of time and energy in the boring process. Consequently,

one might expect each predator to select an optimum size of mussel, one that provides a balance between energy gained from the prey flesh and effort put into obtaining it. Many boring predators do indeed tend to select particular species and sizes of prey, and many position their boreholes in certain areas of the shell in order to minimize the time spent manipulating prey and to maximize the energy returned per unit effort expended. Such parameters have been studied in a variety of boring gastropods from different parts of the world. Feeding rates of *Polinices duplicatus* Say (EDWARDS & HUEBNER, 1977), *Nucella lapillus* Linnaeus (BAYNE & SCULLARD, 1978), and *Natica tecta* Anton (GRIFFITHS, 1981b) have been calculated, while observations on drilling behavior, borehole location, and feeding strategies have been made for *Lunatia alderi* (Forbes) (Verlaine, 1936 quoted by FRETTER & GRAHAM, 1962, and ANSELL, 1960), *Nucella lapillus* (MORGAN, 1972; HUGHES & DUNKIN, 1984), *Natica catena* (da Costa) (NEGUS, 1975), *Thais lamellosa* Gmelin (CAREFOOT, 1977), *Dicathais aegrota* Reeve (BLACK, 1978), and *Natica tecta* (GRIFFITHS, 1981b) among others.

The principal objective of this study is to determine whether *Nucella cingulata* preferentially select prey by species or shell length, and if so, to record the prey preference and consumption rates of predators of various sizes. Observations are also made of the location of boreholes

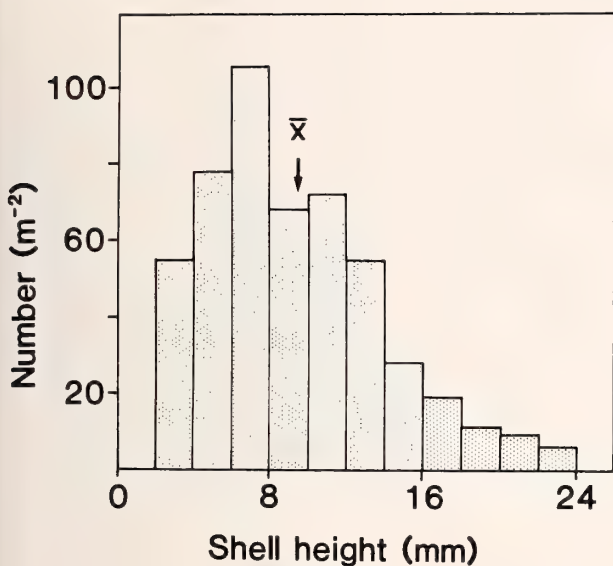


Figure 1

Size-frequency distribution of *Nucella cingulata* on Marcus Island ($n = 336$). Mean density = 492 ± 759 individuals per meter squared.

and relationships between predator and prey size and borehole diameter. The overall energy requirements of the predator population are calculated and compared with the size of the prey resource on Marcus Island. From this, the effect of *N. cingulata* on the mussel population can be determined and the energy requirements of *N. cingulata* compared with those of other mussel predators that occur on the same coast, namely the rock lobster *Jasus lalandii* (Milne Edwards) (GRIFFITHS & SEIDERER, 1980), the boring gastropod *Natica tecta* (GRIFFITHS, 1981b), the starfish *Marthasterias glacialis* (Linnaeus) (PENNEY & GRIFFITHS, 1984), and the African Black Oystercatcher, *Haematopus moquini* Bonaparte (HOCKEY, 1984). Finally, an attempt is made to rate the importance of predation to other population regulating mechanisms.

METHODS AND RESULTS

FIELD STUDIES

A field survey was conducted during April 1983 when a total of thirteen quadrat samples was collected from various tidal levels at each of six study sites on Marcus Island, Saldanha Bay, South Africa ($33^{\circ}02'S$, $17^{\circ}58'E$). The information obtained from each sample included quadrat area, numbers and size distributions of each of the mussel species (*Aulacomya ater*, *Choromytilus meridionalis*, and *Perna perna*), and of the whelk (*Nucella cingulata*), as well as shell length, borehole diameter, and borehole position for drilled shells of each mussel species remaining in the beds. Data from the thirteen quadrat samples have been combined here to give a general pattern for Marcus Island. All correlations have been determined using Pear-

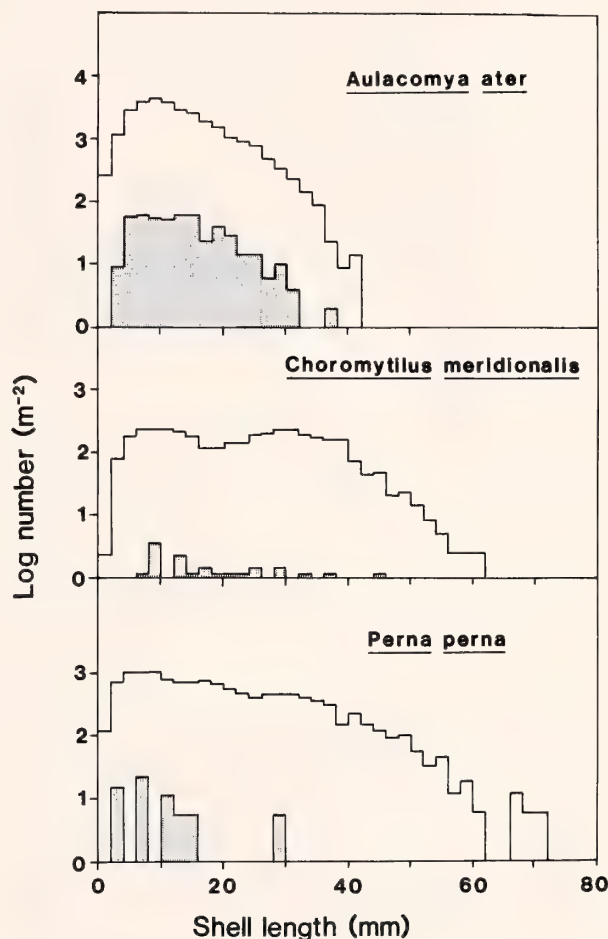


Figure 2

Size-frequency distributions of live and drilled (shaded area) *Aulacomya ater*, *Choromytilus meridionalis*, and *Perna perna* on Marcus Island.

son's product moment correlation coefficient. Mussel size is taken as the distance from the umbo to the opposite tip of the valves. The size of *N. cingulata* is taken as the distance from the base of the shell to the top of the last whorl.

Sizes and Abundances of Predator and Prey and Quantification of Mussel Predation

A size-frequency distribution for *Nucella cingulata* from Marcus Island is shown in Figure 1. The population density was extremely high and extremely variable at 492 ± 759 m^{-2} . Individual size was small, with a mean shell height of 9.5 mm. Size-frequency distributions of both living and drilled *Aulacomya ater*, *Choromytilus meridionalis*, and *Perna perna* are given in Figure 2. Only mussel species are considered here because a negligible number of other drilled invertebrate prey, such as the slipper limpet *Crepidula porcellana* Lamarck, were found. Table 1

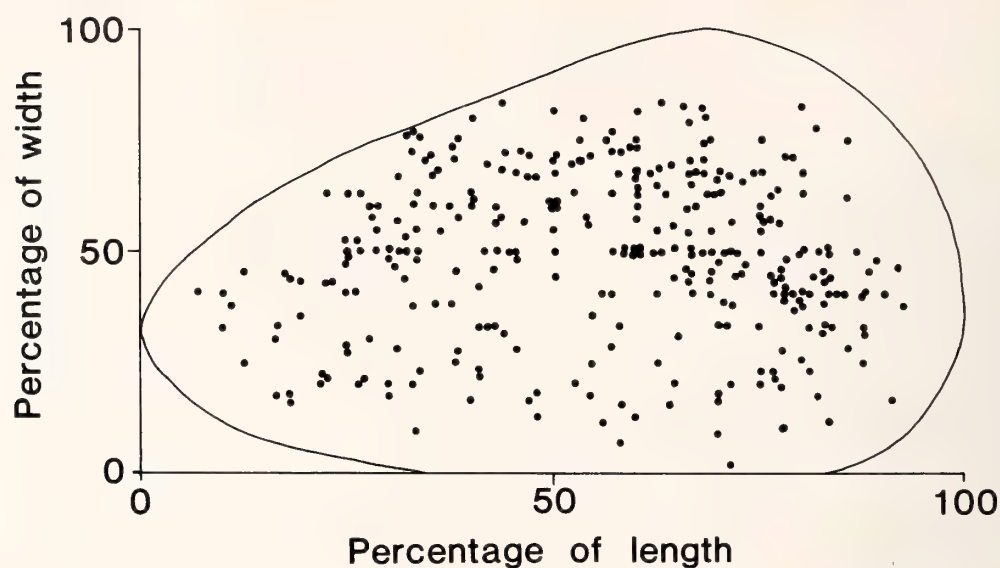


Figure 3

Position of 316 boreholes on *Aulacomya ater* shells collected from Marcus Island.

summarizes the statistics of both living and drilled individuals of the three mussel species. The population size-frequency distributions for *N. cingulata* and all three mussel species are skewed to the right, with the result that the mean size is higher than the population mode. *Aulacomya ater* is the most abundant of the mussel species (64.1%) and appears to be the preferred prey of *N. cingulata* (89.2% of all prey). For all three mussel populations combined, the mean prey size (16.2 mm) is approximately the same as the mean population size (15.5 mm), but drilled *P. perna* were significantly smaller than the population average. *Nucella cingulata* takes similar size ranges of each prey species, although the mean size of *C. meridionalis* taken is slightly greater than that of the other two species.

Location of Boreholes in Shells Collected in the Field

The number of drilled shells of each species and the number of boreholes per drilled shell are given in Table 2. From the total of 323 drilled mussels recovered, there were 24 mussels (7.4%) that had more than one borehole completely penetrating the shell. No *Choromytilus meridionalis* had more than one borehole, but 7.6% of all drilled *Aulacomya ater* and 16.7% of *Perna perna* had been drilled more than once. The position of the borehole on each drilled shell for each of the three species was plotted as the percentage of the shell length against the percentage of the shell width. For *C. meridionalis* and *P. perna*, there were too few borehole data ($n = 23$ and $n = 14$ respec-

Table 1

Population statistics for living and drilled *Aulacomya ater*, *Choromytilus meridionalis*, and *Perna perna* on Marcus Island.

Species	Living populations				Drilled shells				Drilled shells as percentages of their populations
	Density (m ⁻²)	Percentage of all mussels	Mean length (mm)	Size range (mm)	Density (m ⁻²)	Percentage of all mussels	Mean length (mm)	Size range (mm)	
<i>Aulacomya ater</i>	28,528 ± 33,086	64.1	13.0 ± 6.6	1-42	487	89.2	15.7 ± 6.6	3-40	1.74
<i>Choromytilus meridionalis</i>	3593 ± 1823	8.1	22.7 ± 12.0	1-62	16	7.1	21.8 ± 10.2	7-46	0.46
<i>Perna perna</i>	12,356 ± 9738	27.8	19.3 ± 12.6	1-72	62	3.7	12.3 ± 7.1	3-32	0.30
Total	44,477	100.0	15.5	1-72	566	100.0	16.2	3-46	1.27

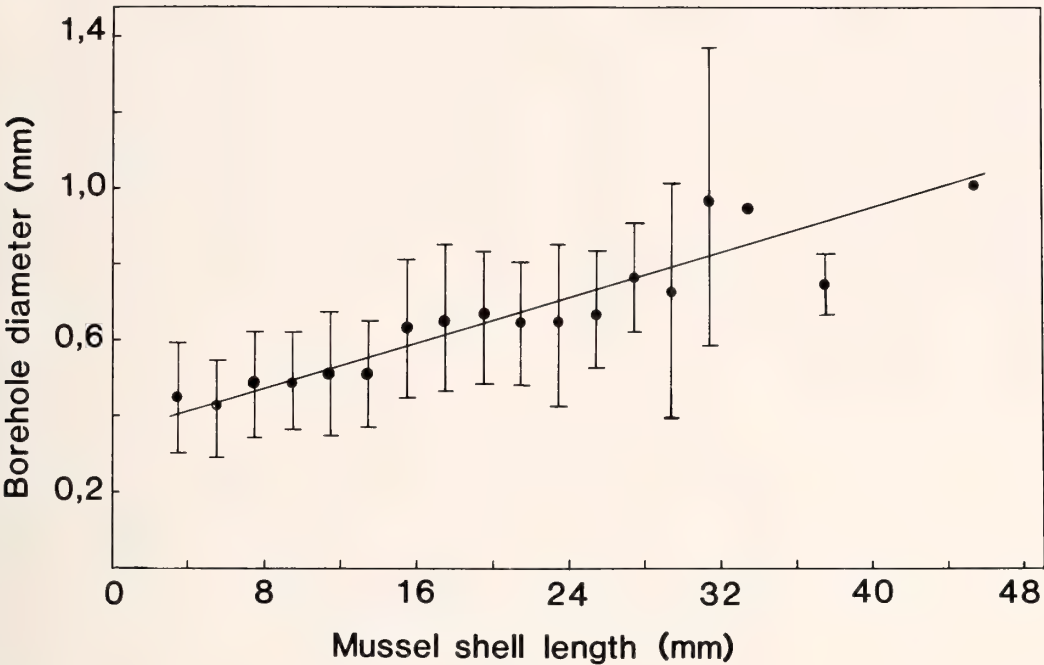


Figure 4

Borehole diameter as a function of mussel shell length for 353 boreholes drilled into all three mussel species collected from Marcus Island. For convenience, a mean value of each 2-mm size class is represented with vertical bars showing one standard deviation either side of this mean.

tively) to show an aggregation in any particular region. Figure 3 shows the borehole positions for *A. ater*. Although the margins of the shell valve are avoided, there does not appear to be a concentration of boreholes in any particular locality. Of the drilled shells of all three species, 48.6% were drilled on the left valve while 51.4% were drilled on the right valve. A chi-square test showed that this difference was not significant ($n = 353$, $0.05 < P < 0.01$).

Borehole Diameter versus Mussel Size

In order to ascertain whether larger mussels had been preyed upon by larger *Nucella cingulata*, borehole diameter was measured and related to the shell length of each drilled mussel. Both outside and inside borehole diameters were measured, but the outside measurement was ultimately used as the standard index of size. Boreholes were measured using a dissecting microscope fitted with a net-scale graduated to 0.1 mm and a mean value calculated for mussels of each 2-mm size class from 3–4 mm to 45–46 mm. Figure 4 shows a plot of mean outside borehole diameter for each 2-mm size class against mussel length. The inside borehole diameter varies less with increasing mussel size, having a slope with half the gradient of that for outside diameter. The correlation between borehole diameter and mussel size is significant ($n = 323$, $0.025 < P < 0.005$), and a regression line fitted to the data gives

the relationship: borehole diameter (mm) = $0.323 + 0.015 \times$ mussel length (mm) ($r = 0.918$).

LABORATORY STUDIES

Because *Aulacomya ater* appeared to be the most abundant prey species taken by *Nucella cingulata*, only this species was considered in our experimental studies. Specimens of *N. cingulata* and *A. ater* were collected from Marcus Island and taken to the laboratory, where prey size-selection and predation-rate experiments were conducted. The an-

Table 2
Number of boreholes found in shells of *Aulacomya ater*, *Choromytilus meridionalis*, and *Perna perna* collected from Marcus Island.

Species	Number of holes in shell					Total number of boreholes	Total number of drilled shells
	1	2	3	4	5		
<i>Aulacomya ater</i>	266	18	3	0	1	316	288
<i>Choromytilus meridionalis</i>	23	0	0	0	0	23	23
<i>Perna perna</i>	10	2	0	0	0	14	12
Total	299	20	3	0	1	353	323

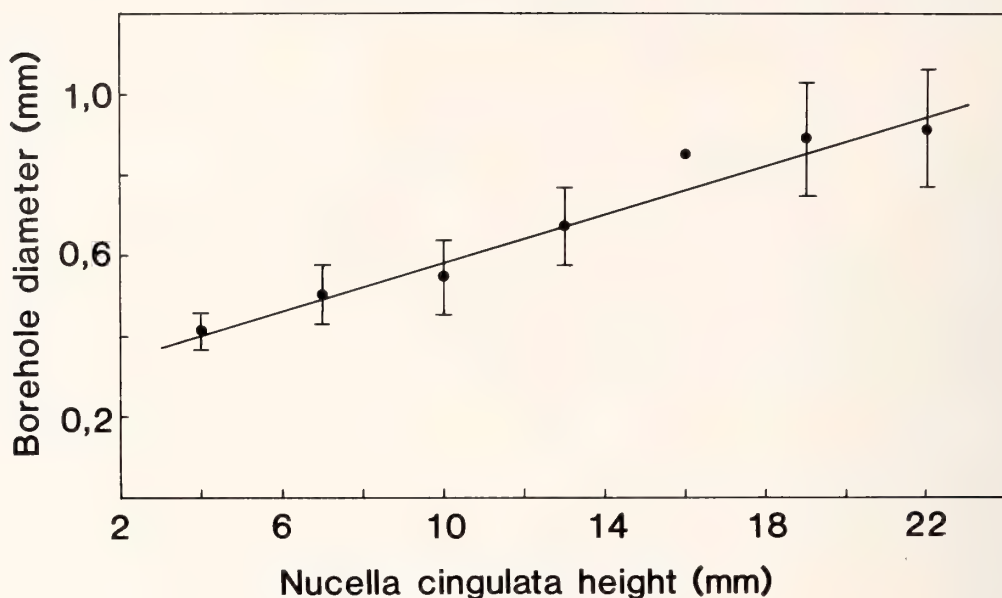


Figure 5

Borehole diameter as a function of *Nucella cingulata* height for 78 boreholes drilled into *Aulacomya ater* shells in the laboratory. For convenience, a mean value for each 2-mm size class is represented here with vertical bars showing one standard deviation on either side of this mean.

imals were maintained in large aquaria connected to a flow-through seawater system at a constant temperature of 14.5°C (which is approximately the temperature of the seawater at Marcus Island). An acclimation period of 15 days was allowed during which time the specimens of *N. cingulata* were supplied with excess *A. ater* of a wide size range. The whelks ($n = 33$) were then separated into seven 3-mm size classes (3–5 mm to 21–23 mm), each group being placed in a separate plastic floating ring with a net base and floated in a large tank. In two of the size classes of *N. cingulata* only a few individuals were available, so not all of the rings were initially supplied with the same number of individuals. The specimens of *A. ater* were also separated into eight 5-mm size classes (1–5 mm to 36–40 mm) and each of the seven rings supplied with six individuals from each size class of mussel.

The tanks were subsequently examined every 4 days for a total period of 32 days. At each sampling all the drilled mussels were removed and measured and replaced with other individuals from the same size class. Any dead individuals of *N. cingulata* were also removed and, where possible, replaced with other individuals from the same size class. Additional specimens of *N. cingulata* were kept in a separate tank and were fed *Aulacomya ater* to sustain them, so that they would not be starved if needed in the experiments. Because the number of predators per size class during each 4-day sampling period was not constant, the consumption rate per *N. cingulata* was calculated independently over each 4-day period and subsequently averaged.

Location of Boreholes in Shells Collected in the Laboratory

No shell with more than one complete borehole was found during the laboratory experiments. The positions of the boreholes were similar to those in shells recovered from the field. Of the drilled shells, 42.3% were drilled on the left valve and 57.7% on the right valve. A chi-square test showed that this difference was not significant ($n = 78$, $0.05 < P < 0.01$).

Borehole Diameter versus *Nucella cingulata* Size

The mean outside and inside borehole diameters were calculated for *Aulacomya ater* shells drilled by *Nucella cingulata* of each of the size classes. The slope for inside diameter against *N. cingulata* size was again half that for outside diameter. A plot of mean outside borehole diameter against *N. cingulata* size is given in Figure 5. The correlation between borehole diameter and *N. cingulata* size is significant ($n = 78$, $0.025 < P < 0.005$), and a regression line fitted to the data produced the relationship: borehole diameter (mm) = $0.281 + 0.03 \times N. cingulata$ height (mm) ($r = 0.980$).

Drilled *Aulacomya ater* Size versus *Nucella cingulata* Size

The mean size of *Aulacomya ater* drilled by *Nucella cingulata* of each 3-mm size class is shown in Figure 6. The correlation between *N. cingulata* size and shell length

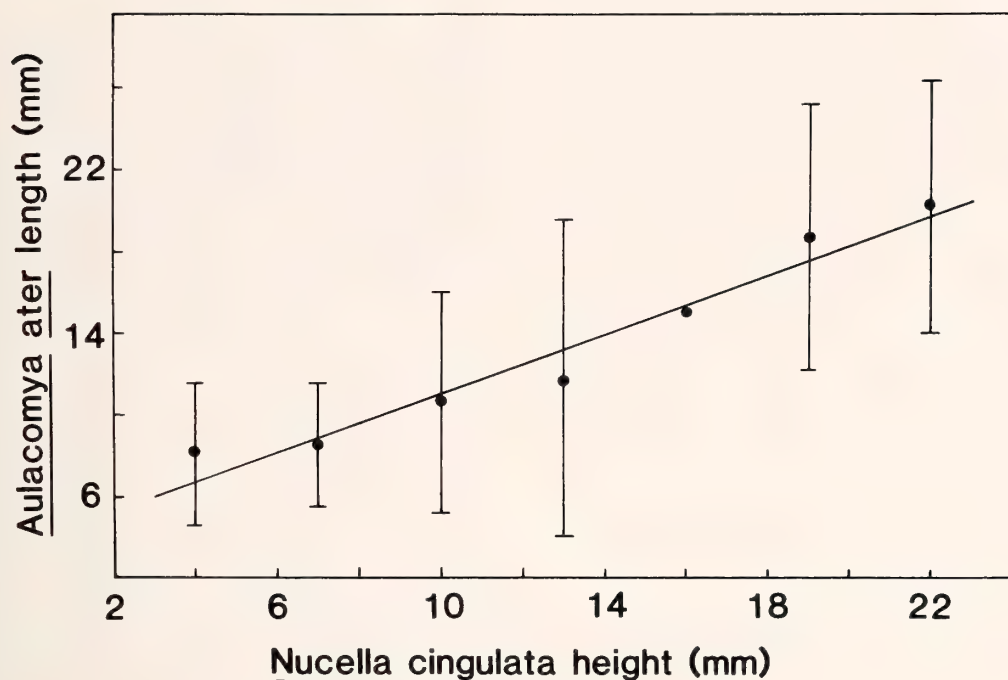


Figure 6

Length of 78 *Aulacomya ater* consumed in a laboratory experiment as a function of *Nucella cingulata* height. For convenience, a mean value for each 2-mm size class is represented here with vertical bars showing one standard deviation on either side of this mean.

of prey taken is significant ($n = 78$, $0.025 < P < 0.005$), and a regression line fitted to the data produced the relationship: $A. ater$ length (mm) = $3.632 + 0.734 \times N. cingulata$ height (mm) ($r = 0.978$).

Predation Rate

Number of prey consumed: For each *Nucella cingulata* size class, the number of *Aulacomya ater* consumed per individual per day was calculated (Table 3). The mean consumption rate was 0.08 ± 0.035 , but there was no apparent relationship between the number of prey consumed per day and predator size.

Energy consumption: The dry flesh weights of different sized specimens of *Aulacomya ater* (5–25 mm) were measured, and the energy value of the flesh was determined by bomb calorimetry. The relationship between *A. ater* dry weight and size is significant ($n = 90$, $0.025 < P < 0.005$), the relationships being: (1) $A. ater$ dry weight (mg) = $0.025 \times A. ater$ length (mm)^{2.358} ($r = 0.889$) and (2) $A. ater$ energy value = 18.27 ± 0.95 kJ/g dry weight.

Because no flesh appeared to remain behind in the discarded mussel shells, it was assumed that *Nucella cingulata* ingests its prey with 100% efficiency. Contrary results have been found in, for example, *Polinices duplicatus*, which consumes only the visceral portion of the clam *Mya arenaria* Linnaeus (EDWARDS & HUEBNER, 1977), and we

recognize that there is likely to be loss of some semiliquid material (e.g., DAGG, 1974); however, we were unable to quantify this. Thus, for each size class of *N. cingulata*, all the *Aulacomya ater* drilled in each of the eight 4-day sampling periods were converted to energy equivalents, and the total amount of energy consumed per predator in each 4-day period was calculated. These values were then summed to give the total energy consumed per *N. cingulata* over the 32 days and converted to weekly energy values. A plot of energy consumed per *N. cingulata* per week

Table 3

Number of *Aulacomya ater* consumed per *Nucella cingulata* individual per day in laboratory experiments.

<i>Nucella cingulata</i> size class (mm)	Number of <i>Aulacomya ater</i> consumed per individual per day
3–5	0.07
6–8	0.12
9–11	0.11
12–14	0.10
15–17	0.02
18–20	0.07
21–23	0.05
Mean \pm 1 SD	0.08 ± 0.035

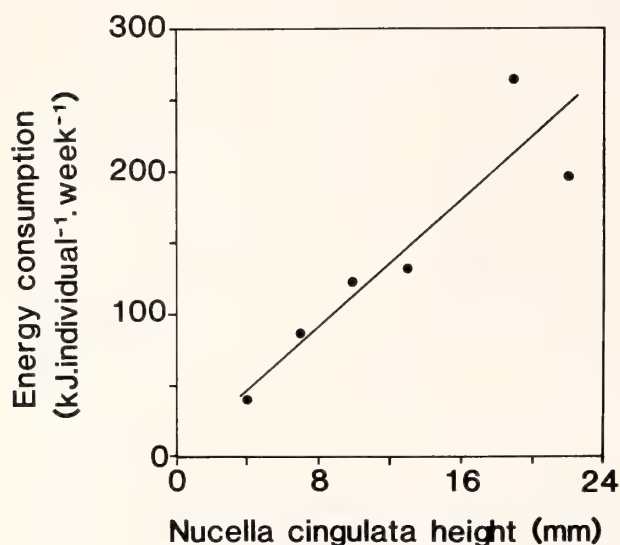


Figure 7

Average weekly energy consumption of *Nucella cingulata* during the laboratory experiments as a function of shell height.

against *N. cingulata* height is shown in Figure 7. One *N. cingulata* size class yielded only two data points and this group was excluded from the analysis. The correlation between mean energy consumption per week and *N. cin-*

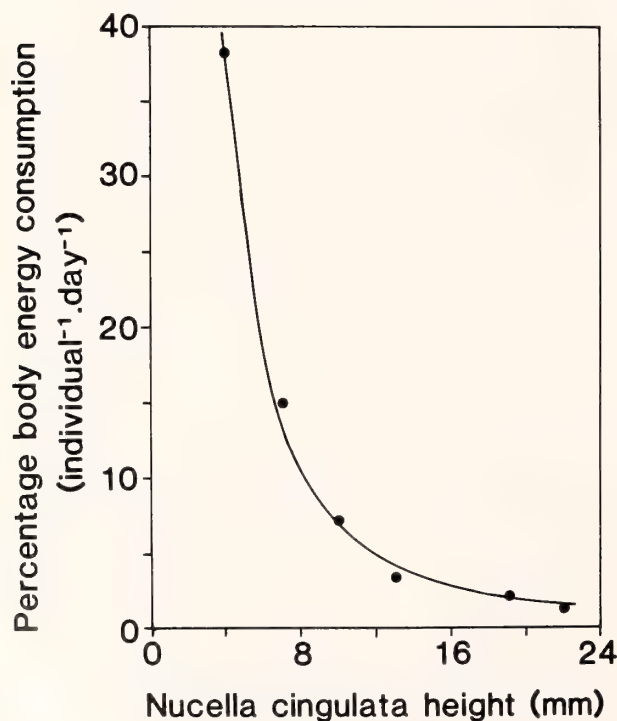


Figure 8

Percentage body energy consumption per *Nucella cingulata* individual per day as a function of shell height.

gulata size is significant ($n = 6$, $0.025 < P < 0.005$), and regression of the data produced a power curve with the relationship: energy consumption (kJ/week) = $1.187 \times 10^{-2} \times N. cingulata$ height (mm) $^{0.98}$ ($r = 0.967$).

Percentage body energy consumed by *Nucella cingulata*: The dry weights of different sized specimens of *Nucella cingulata* (6–25 mm) were measured, and the energy value of the flesh was determined by bomb calorimetry. The correlation between *N. cingulata* dry weight and size is significant ($n = 29$, $0.025 < P < 0.005$), the relationships being: (1) *N. cingulata* dry weight (mg) = $0.012 \times N. cingulata$ height (mm) $^{2.999}$ ($r = 0.984$), and (2) *N. cingulata* energy value = 20.52 ± 0.04 kJ/g dry weight.

From these equations, the energy values of *N. cingulata* of different sizes were calculated. Using the daily consumption rates in conjunction with the energy values of *N. cingulata*, the percentage body energy consumed per day for different sized specimens of *N. cingulata* was obtained. A plot of percentage body energy consumed per day by different sized *N. cingulata* is given in Figure 8. The correlation between percentage body energy consumed and *N. cingulata* size is significant ($n = 6$, $0.025 < P < 0.005$), and fits a power curve with the relationship: percentage body energy consumed per individual per day = $5.263 \times 10^2 \times N. cingulata$ height (mm) $^{-1.912}$ ($r = -0.996$).

DISCUSSION

Prey Selection

Our field surveys showed that *Nucella cingulata* preys upon all three of the mussel species present on Marcus Island. *Aulacomya ater* appears to be the preferred prey because it comprises 64% of the living mussel community, but makes up 89% of the natural diet of *N. cingulata* (as indicated by numbers of drilled shells found in the field). There are several possible reasons for this preference for *A. ater*. It may be selected simply because it is the most abundant and hence most easily located prey species. The tidal level at which *N. cingulata* is most abundant is that at which *A. ater* is most dense. This may be because of similar tolerance of the two species to exposure, rather than simply an aggregation of predators in the region of maximum prey availability. One factor that certainly contributes to the greater vulnerability of *A. ater* is that the population consists almost entirely of small individuals (<40 mm) that fall within the size range available as prey to *N. cingulata* (3–46 mm). By contrast, many of the specimens of *Choromytilus meridionalis* and *Perna perna* exist in a "refuge in size" (PAINE, 1965) over 46 mm, where they are not available to the small individuals of *N. cingulata* that dominate the population in this area. There is no doubt, however, that there is a definite preference for *A. ater* even within the available size range as prey, as can be seen from Figure 2.

Laboratory experiments showed that the size of prey taken by individual *Nucella cingulata* is an increasing func-

tion of predator size (Figure 6), a finding that is confirmed by studies of other boring gastropods, such as *Nucella lapillus* (BAYNE & SCULLARD, 1978) and *Polinices duplicatus* (EDWARDS & HUEBNER, 1977). The size of predators can also be inferred from borehole diameter (Figure 5), so our laboratory results could be validated in the field by correlating borehole diameter with length of drilled mussels. Field surveys indeed confirmed that larger mussels had, on average, wider boreholes (Figure 4) and, hence, had been preyed upon by larger predators.

Location of Boreholes

Some boring gastropods selectively drill in a particular location of the prey shell. CAREFOOT (1977), for example, calculated that 98% of the boreholes drilled by *Thais lamellosa* on *Mytilus edulis* were found in the thinner regions of the prey shell, whereas HUGHES & DUNKIN (1984) found that *Nucella lapillus* reduced drilling time by approximately 27% by drilling through the thinnest areas of the shell. GRIFFITHS (1981b) found that the position of the boreholes drilled by *Natica tecta* on *Choromytilus meridionalis* were related to the way in which the predator holds its prey. MORGAN (1972) showed that the boreholes on *Cerastoderma edule* drilled by *Nucella lapillus* were determined by the way the cockle is held in the sand. *Thais lamellosa* (CAREFOOT, 1977), *Lunatia alderi* (Verlaine, 1936 quoted by FRETTER & GRAHAM, 1962), *Dicathais aegrota* (BLACK, 1978), and *Nucella lapillus* (HUGHES & DUNKIN, 1984) have been shown to drill boreholes over particular underlying organs. However, the boreholes drilled by *Nucella cingulata* appear to be randomly located over the entire central portion of the shell, with no preference for either valve. Several *Nucella lapillus* individuals have been observed to feed simultaneously on a single prey item (MORGAN, 1972; BAYNE & SCULLARD, 1978). Because 7.4% of all mussels drilled by *N. cingulata* on Marcus Island have more than one hole, it is possible that this may have resulted from a cluster of individuals feeding at the same time. Alternatively, some *N. cingulata* may, in error, drill into a mussel that has already been eaten, particularly if the mussel has not opened because of incomplete ingestion of the adductor muscle by the original attacker.

Predation Rate

The number of *Aulacomya ater* individuals consumed by *Nucella cingulata* shows no increase with predator size, the increased consumption rates of larger predators being attained by eating larger prey, rather than by taking more of them. Energy consumption is an approximately linear function of *N. cingulata* height (power value of 0.98). This is in contrast to the findings for *Natica tecta*, where energy consumption is approximately a cubic (power value of 2.9132) function of shell height (GRIFFITHS, 1981b). The two shells are, however, quite different in shape, *Natica tecta* having a more spherical shape and presumably in-

creasing in weight more rapidly with shell height. *Nucella cingulata* consumption, moreover, declines drastically from about 40.0 to 1.5% of body energy per day with increasing size, over the range of 3 to 23 mm (Figure 8). By comparison, BAYNE & SCULLARD (1978) showed that *Nucella lapillus* consumes between 15 and 1.5% of its body weight per day over a size range of 12 to 32 mm, while *Polinices duplicatus* consumes between 1.3 and 0.9% of its body weight per day over a size range of 19 to 45 mm (EDWARDS & HUEBNER, 1977). The lower limits of the percentage body energy/weight consumed for the larger animals of these different species are comparable, while the smaller specimens of *N. cingulata* take a greater percentage, as might be expected as a result of their higher weight-specific metabolic rate.

Exploitation of *Aulacomya ater* on Marcus Island

Using our laboratory relationship between energy consumption and size of *Nucella cingulata*, together with its size-frequency distribution and density on Marcus Island, the energy requirement of the entire population can be calculated as $3475 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. The standing crop of the entire *Aulacomya ater* population was $7939 \text{ kJ} \cdot \text{m}^{-2}$, while the energy available from individuals in size classes accessible to *N. cingulata* is $7437 \text{ kJ} \cdot \text{m}^{-2}$ (94% of the total). It is of interest to compare this predation rate with those of other mussel predators that occur in the same area. *Aulacomya ater* comprises only 16% of the diet of the African Black Oystercatcher, *Haematopus moquini*, on Marcus Island and its total annual take of mussels is estimated to be a relatively moderate $878 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (HOCKEY, 1984, and unpublished data). Three invertebrate predators, the rock lobster *Jasus lalandii*, the starfish *Marthasterias glacialis*, and the gastropod *Natica tecta* have also been studied. In their areas of maximal abundance and when feeding on the mussel *Choromytilus meridionalis*, these were predicted to consume annual totals of $5835 \text{ kJ} \cdot \text{m}^{-2}$, $6028 \text{ kJ} \cdot \text{m}^{-2}$ and $9010 \text{ kJ} \cdot \text{m}^{-2}$ respectively (PENNEY & GRIFFITHS, 1984). Populations of *C. meridionalis*, however, have a greater standing crop ($19,125\text{--}21,675 \text{ kJ} \cdot \text{m}^{-2}$) than those of *A. ater*, so that the percentage of standing crop taken in each case is remarkably similar, at 46% for *N. cingulata* consuming *A. ater* and between 28 and 44% for the three predators of *C. meridionalis*.

Although we recognize that laboratory feeding experiments may substantially overestimate consumption rates, the predation pressure exerted by each of these predators is nevertheless considerable and, if there were no mussel replacement, they would rapidly obliterate their prey populations. In reality, however, each species has been studied in its area of maximum abundance and there is only partial overlap in the distributions of the various species. Therefore, where one predator is particularly abundant, the others are often rare or absent, and where two or more predators are present, they frequently both occur at reduced densities. Nonetheless, our results suggest that pre-

dation rates of 30–50% of prey standing stock per annum are commonplace and these would significantly affect the density and size composition of the mussel beds, particularly because the majority of prey are taken from a particular "window" of size classes available to the predators.

If we consider the overall impact of predation on settlements of mussels, however, we must remember that juvenile mussel populations have an extremely high production-to-biomass (P/B) ratio which allows them to support considerable predation pressure without any decline in standing crop. In *Aulacomya ater*, for example, the P/B ratio is 29.5 at 5 mm (all of which goes into growth), declining below 2.0 above 45 mm (most of which is expended in reproductive output) (GRIFFITHS & KING, 1979). Secondly, GRIFFITHS (1981a) has shown that juvenile *Choromytilus meridionalis* normally settle at densities of some tens of thousands of individuals per square meter, whereas the maximum packing density of adults over 50 mm is of the order of one thousand per square meter. These figures may not be directly applicable to *A. ater*, which can form multilayered beds, but a mortality of 90% or more is still to be expected over this growth period and will be accomplished by intraspecific competition for space should there be little or no mortality through predation.

Populations of juvenile mussels can thus absorb considerable losses to predation while remaining at maximum population density in terms of substrate carrying capacity. The actual rate of loss that can be tolerated while maintaining 100% cover will vary with the growth rate, but will probably be at least equal to the standing crop, because the P/B ratio of mussels of the size range available to predators is at least two. It is interesting to note that at the point where mussels grow into a "refuge in size," when they are no longer available to the majority of predators, they almost simultaneously arrive at a stable packing density at which they can continue to grow in length while fitting into the same area of substrate (see GRIFFITHS, 1981a, fig. 7).

In conclusion then, it appears that dense settlements of juvenile mussels can support large populations of predators during their logarithmic growth phase, while maintaining complete substrate coverage and constant or even increasing biomass and reproductive output (GRIFFITHS, 1981a). The slowing of growth rate that occurs as adult size is approached is accompanied by reductions both in the intensity of competition for space and in predation pressure, because the mussels reach a size at which they are relatively immune to predators. These adult populations persist until they become senile and die or are eliminated by some natural catastrophe, which may often take the form of a massive settlement of their own spat (GRIFFITHS, 1981a).

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The Activity Pattern of *Onchidella binneyi* Stearns (Mollusca: Opisthobranchia)

by

PHILIP J. PEPE AND SUEANNE M. PEPE

Center for the Study of Deserts and Oceans, P.O. Box 53, Puerto Peñasco, Sonora, Mexico

Abstract. *Onchidella binneyi* inhabits the upper intertidal zone on rocky shores of the Gulf of California. At El Bajo, B.C.S., Mexico, the activity of a population of *O. binneyi* followed a distinct pattern. The nightly activity period began shortly after the ebbing tide exposed the animals' position on the shore. The number of active animals increased steadily to a maximum and then declined until all activity ceased during the hour of low tide.

The activity cycles of *Onchidella binneyi* were synchronous with the tides. The maximum number of animals active each night was inversely correlated with the tidal height at low tide. At neap tides the *O. binneyi* population was inactive. At spring tides the intensity of activity reached a maximum.

Animals were held in aquaria in a non-tidal simulation. They continued to exhibit daily activity very similar to the field population. This indicates that either the population is directly cued by some environmental factor that fluctuates in relationship to the tides, or that *Onchidella binneyi* possesses an internal biological clock.

INTRODUCTION

Onchidella is a small genus of opisthobranchs that has a wide geographical distribution. Members of this genus are completely shell-less as adults, with papillate mantles and lungs (WATSON, 1925; FRETTER, 1943). Their mantle margins contain repugnatorial glands whose secretions are effective against a wide range of possible predators including crabs and fish (AREY & CROZIER, 1921; WATSON, 1925; IRELAND & FAULKNER, 1978). *Onchidella* inhabits rocky shores, living in eroded cavities or clefts between stones (AREY & CROZIER, 1921; WATSON, 1925; FRETTER, 1943; MARCUS & MARCUS, 1956). With few exceptions, species of *Onchidella* have been reported only from the intertidal zone.

Activity patterns synchronous with ocean tides have been reported for four species of *Onchidella*: *O. verruculatum* Cuvier (HIRASKA, 1912), *O. floridanum* (Dall) (AREY & CROZIER, 1921), *O. celtica* (Forbes & Hanley) (FRETTER, 1943), and *O. indolens* (Gould) (MARCUS & MARCUS, 1956). In each case animals were observed crawling about on the top surfaces of rocks during daytime ebbing tides only. During other tidal stages, they were not observed on the surface of the rocks but were found inactive within rock cavities.

AREY & CROZIER (1921) observed *Onchidella florida-*

num on Bermuda shores and reported a diurnal activity pattern for this species. *Onchidella floridanum* emerged from its rock shelters only after the falling tide had left it exposed to the air for approximately one hour. Individuals were observed actively grazing diatoms on the rock surfaces for an additional hour. After the grazing period, the animals simultaneously returned to their shelters. All animals had disappeared from the top surfaces of rocks before low tide.

Onchidella binneyi Stearns, 1893, a dark gray slug approximately 2.5 cm long, is endemic to the Gulf of California. Preliminary observations in May 1978 indicated that *O. binneyi*, although active only at night, had an activity pattern similar to that of *O. floridanum*. A study was designed to determine whether the activity of a population of *O. binneyi* was synchronous with ocean tides and whether the behavior would persist if animals were left in standing seawater in aquaria.

STUDY AREA

The study area was located at El Bajo, 10 km north of Loreto, Baja California Sur, Mexico, on the shore of the central region of the Gulf of California. At El Bajo the upper intertidal zone consists of densely packed basalt boulders and shingles over a sand base. The beach slopes

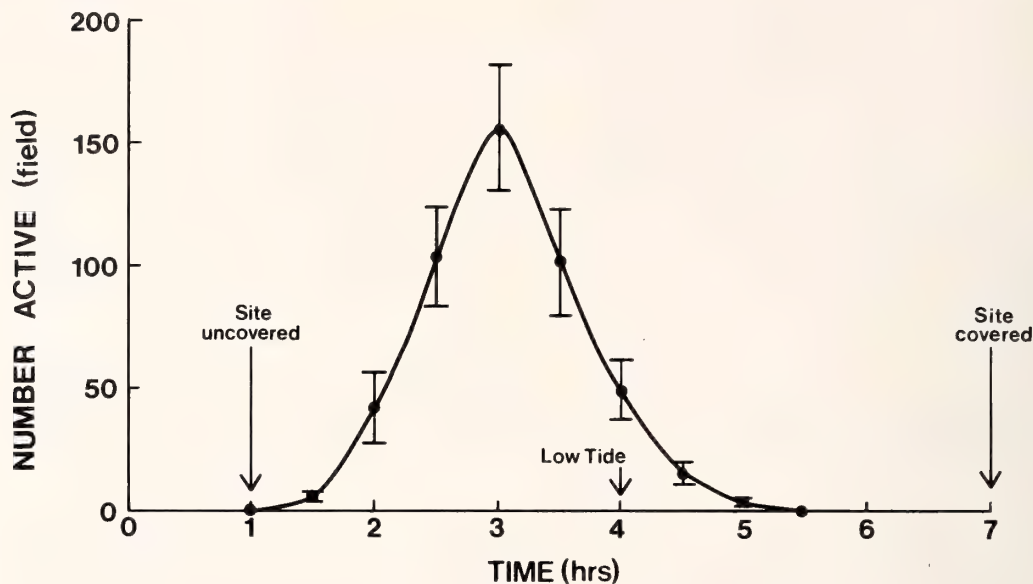


Figure 1

The mean number of active animals during 25 nights of activity for the *Onchidella binneyi* population at El Bajo, B.C.S., Mexico. The bars represent the standard errors of the mean. The arrows indicate the average time of the animals' exposure to the air and the average time of low tide relative to the activity of the population.

about 4° seaward. *Onchidella binneyi* lives in a narrow zone buried beneath the stones. This zone is located at a tidal height of approximately 0.8 m above mean lower low water (MLLW). El Bajo is protected from storm surge by a nearby offshore island, Isla Coronado.

The central region of the Gulf of California has mixed semi-diurnal tides that change to a diurnal pattern during the neap portion of a tidal series. At El Bajo the maximum tidal range is approximately 1.4 m. The tides at El Bajo match the NOAA predictions for Guaymas, Sonora, Mexico.

Onchidella binneyi lives just below mean sea level (MSL), or the break between the high and middle intertidal zones as defined by RICKETTS & CALVIN (1939). Therefore, the population experiences one or occasionally two aerial exposures per day during the spring portions of a tidal series, and zero or one exposure per day during the neap portions.

METHODS

At El Bajo, the *Onchidella binneyi* population is restricted to a 2-m wide strip parallel to the drift line. A 20-m long section of this strip was marked for observation. To avoid disturbing the animals' natural activities, the area was studied from its perimeters only, and animals were never removed from it. Observations were made from 5 to 21 August 1978 and from 10 to 24 May 1979.

Specimens of *Onchidella binneyi* observed on the tops and sides of rocks were considered active (WELLS [1980] followed a similar definition for limpets). The number of

active animals was recorded every 30 min. Counts were begun when the falling tide first uncovered the marked area and were continued until animals were no longer observed on rock surfaces. The tidal height and time of low tide were also recorded. Nighttime observations were made using flashlights. Two independent counts were conducted simultaneously to ensure accuracy. A light-dark preference experiment showed that the slugs' movements were not affected by the flashlights.

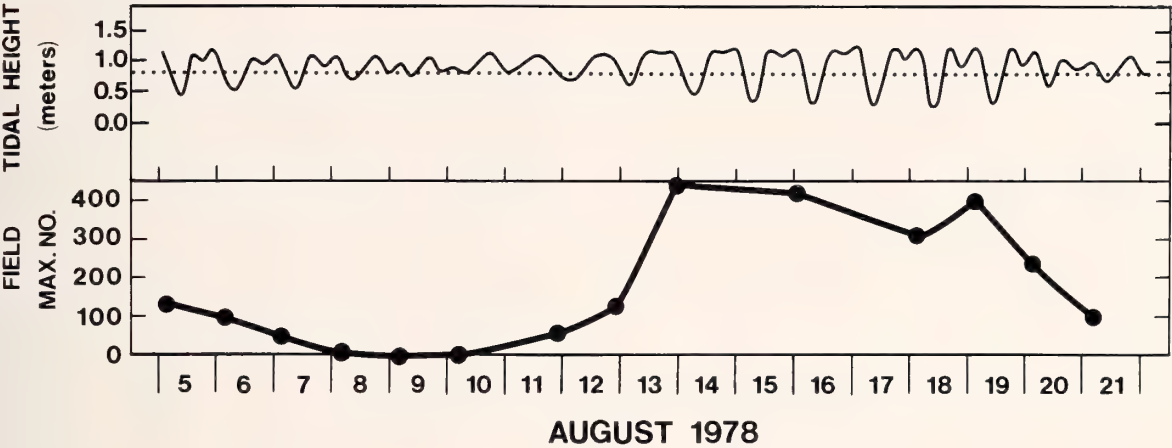
A set of experiments was run from 13 to 19 May 1979 to determine whether the activity pattern would persist if the animals were left submerged in seawater. Three 1-L jars (16 cm tall) with screen tops were used as aquaria. Ten specimens of *Onchidella binneyi* were placed in each jar and the jars were filled with seawater to within 4 cm of the top. The water was partially changed each day but never totally drained, thus simulating a non-tidal condition. The aquaria were shaded from the sun. The number of active slugs and the time of activity were recorded periodically for the experimental and field populations simultaneously.

RESULTS

Behavior Synchronous with the Tides

Onchidella binneyi was active only at night when exposed to the air. During these activity periods the animals had a particular appearance: their mantle margins were lifted above the substrate; their eyestalks were extended and their oral lobes were swept from side to side; and

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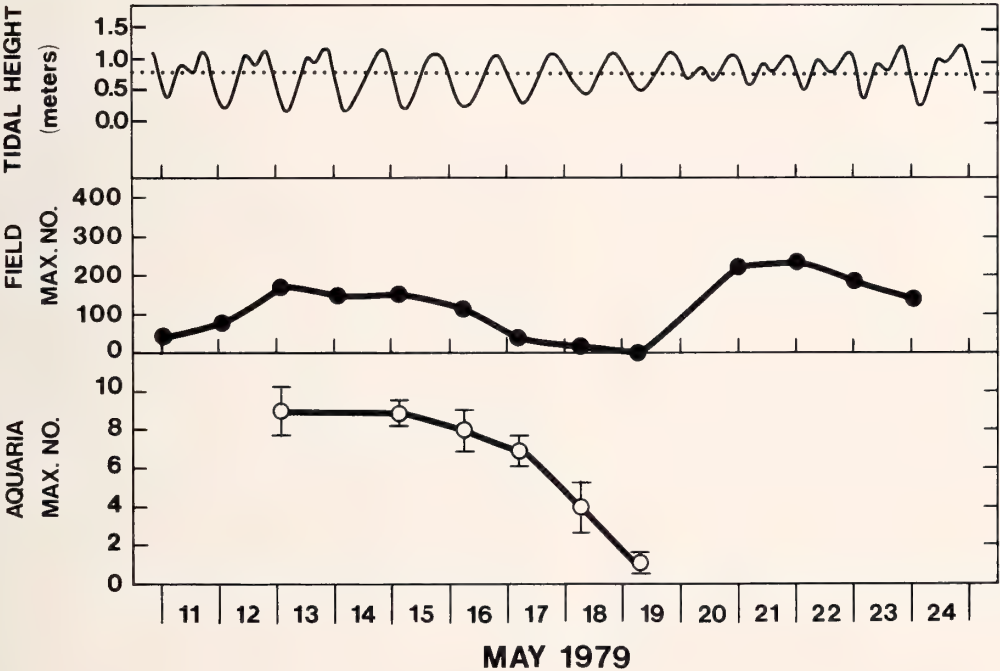


Figure 2

The intensity of nightly activity (maximum number active) is compared with the tidal amplitudes (NOAA predictions for Guaymas, Mexico) and the lunar phases for each census period. The August and May graphs both report data for the field population (closed circles). Each point represents a single night's maximum count. The May graph reports data for the experimental population in the aquaria (open circles). Each experimental point represents the mean of three replicates and includes standard error bars. The horizontal dotted lines through the tidal amplitudes depict the tidal height of the animals' position on the shore.

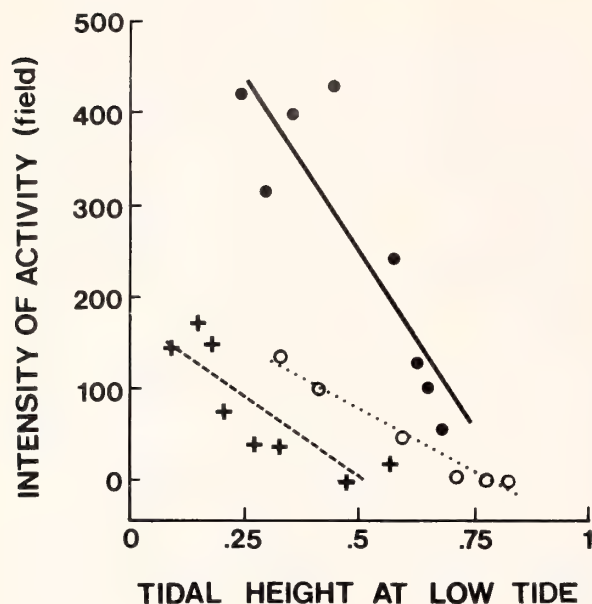


Figure 3

The relationship between the intensity of activity (maximum number active) in the field population and the predicted tidal height at low tide. Each point represents one night of the census period. Regression lines are fitted to the data points for each of three tidal series. August 5 to 10, 1978 (part of a new moon tidal series) is depicted with open circles and a dotted line ($r^2 = 0.98$). August 11 to 21, 1978 (part of a full moon tidal series) is depicted with closed circles and a solid line ($r^2 = 0.77$). May 11 to 19, 1979 (part of a full moon tidal series) is depicted with crosses and a dashed line ($r^2 = 0.72$).

their dorsal surfaces were flat and mantle papillae were retracted. Activities included grazing on diatom films, copulating, and moving about at an average speed of 2 cm/min (determined by measuring the distance covered during 1 h for 10 animals).

During the active periods, individual animals were observed on the upper surfaces of the rocks for durations of from 1 min to over an hour. The animals did not emerge or retreat simultaneously. Instead animals moved between active and inactive portions of the population.

The number of animals active on the surface followed a particular pattern each night. The active period began shortly after the ebbing tide uncovered the study area. The number of animals on the surface increased steadily to a maximum and then declined until all activity ceased during the hour of low tide (Figure 1).

The time of the active period progressed during a tidal series in the same manner as the tides (approximately 0.8 h each night). Maximum activity occurred an average of 1 h before low tide. The time between successive peaks of activity was not significantly different from the duration of a lunar day (24.8 h), averaging 24.6 ± 0.5 h (\pm SD; t -test, $P = 0.5$, $n = 20$).

The intensity of activity (maximum number of animals active each night) followed the monthly variation in the amplitude of the tides (Figure 2). These maximum numbers were inversely correlated with the tidal heights at low tide in both August and May ($r^2 \geq 0.72$, 95% confidence) (Figure 3). The data were divided into new and full moon tidal series for this analysis because they were separated by days having neap tides (August 10, May 19). These dates marked the division between fortnightly activity cycles when the moon was in the first and last quarters, respectively, and *Onchidella binneyi* was inactive.

Repeated attempts were made to find slugs during daytime ebbing tides, and when their zone was submerged. Although no surface activity was observed on these occasions, animals were found by turning over rocks adjacent to the marked study area. These slugs were inactive and huddled together in small groups. The inactive animals had their eyestalks and oral lobes retracted, their dorsal surfaces highly arched, and their mantle papillae extended, giving them a frilly appearance. Inactive slugs were never observed copulating (WEBB *et al.* [1969] reported a similar finding for *Onchidella peronii*).

Behavior Independent of Tidal Cues

The daily activity cycles of *Onchidella binneyi* held in aquaria were very similar to those of the field population (Figures 1, 4). When inactive, the slugs huddled together on the bottoms of the jars, and exhibited the characteristic frilly appearance. When active, they crawled up the sides of the jars, above the waterline, and made grazing attempts on the glass with their radulae. Animals were considered active when observed at least 4 cm above the bottom of their jar.

The details of the activity cycles of the experimental group were compared to those of the field population. There was no significant difference between the mean time at which the first animals became active in the aquaria and in the field (t -test, $P = 0.4$, $n = 18$). The mean time at which the maximum activity occurred was also not significantly different between the experimental and field populations (t -test, $P = 0.4$, $n = 18$).

DISCUSSION

Onchidella is behaviorally adapted to the intertidal environment. When the slugs are submerged in seawater their lungs are inoperative and they depend upon diffusion of gases through the mantle surface. The metabolic demands of locomotion cannot be met during submergence and activity is severely limited (FRETTER, 1943; DENNY, 1980). Feeding excursions and sexual activities are curtailed. In addition, *Onchidella* does not have the ability to clamp tightly to rocks, and is easily dislodged by wave surge (AREY & CROZIER, 1921; MARCUS & MARCUS, 1956). When submerged in seawater, *Onchidella* must spend its time buried under rocks. When exposed to the air, pul-

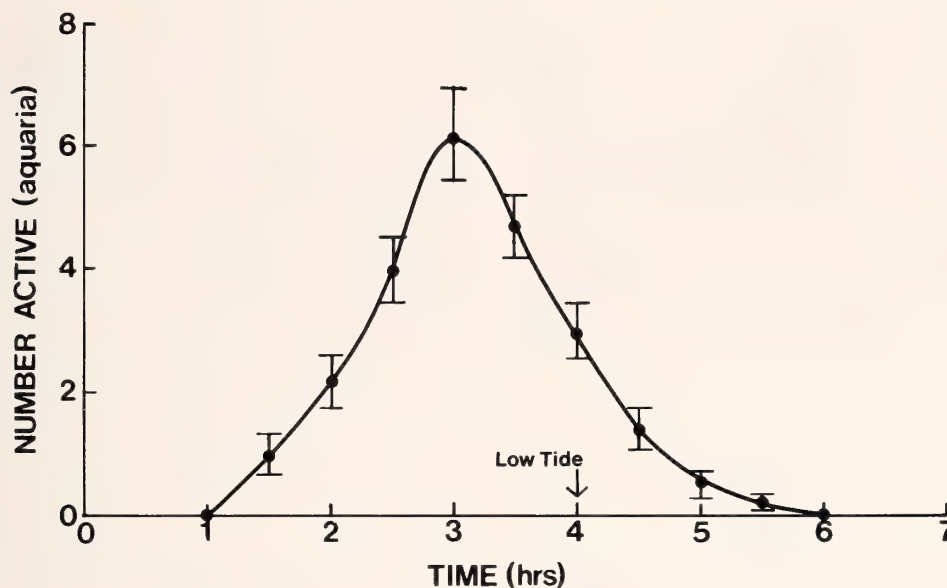


Figure 4

The mean number of active animals during six nights of activity for the experimental population of *Onchidella binneyi* held in three 1-L jars filled with seawater (10 animals per jar). Each point is the mean of three replicates for all six nights of the experiment ($n = 18$). The bars represent the standard errors of the mean. The arrow indicates the average time of low tide relative to the activity of the experimental population.

monary respiration supplements pallial diffusion and the slugs are able to crawl on the top surfaces of rocks where they feed on diatom films, seek mates, and copulate. However, their foraging time is limited. *Onchidella* is shell-less and subject to dehydration and loss of pulmonary capabilities if not submerged periodically (AREY & CROZIER, 1921; FRETTER, 1943). They will die if exposed to warm, dry air for prolonged periods. Therefore, *Onchidella* must live at a level on the shore that is alternately exposed and submerged. When the tide ebbs they must emerge, forage on rock surfaces, and return to cover before the tide rises and floods their position on the shore.

Onchidella binneyi is faced with a choice when its position on the shore is exposed to the air. The slugs can maximize their feeding rate and frequency of copulation by staying on the surfaces of rocks or they can minimize the risks of dehydration and being dislodged by waves by returning early to cover. Theoretically, the animals that would live longest and leave the most offspring would be those that emerge early and return to cover at the appropriate time to balance risks and rewards (SPIGHT, 1982).

To optimize foraging behavior, *Onchidella binneyi* would have to match its activity to the fortnightly tidal pattern. The duration of aerial exposure of the slugs' zone changes during a tidal cycle. At neap tides, the water level either does not drop below their zone at all, or drops barely below it for up to only 4 h. At spring tides, the water level drops well below the slugs' level on the shore and exposure lasts for 6 to 8 h. As the tides progress from neap to spring, the *O. binneyi* population becomes more and more

active, seemingly taking advantage of the longer exposure periods. As the tides progress from spring to neap, the population becomes less active, seemingly to avoid the risks of wave action.

The activity rhythm of *Onchidella binneyi*, with its period of a lunar day, is probably a circalunadian rhythm, as defined by PALMER (1974). The activity patterns of the *O. binneyi* population are synchronous with the tides and its nightly activity persists when left in standing seawater in aquaria. This indicates that either the population is directly cued by some other environmental factor that fluctuates in relationship with the tides, or that *O. binneyi* possesses an internal biological clock.

ACKNOWLEDGMENTS

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A Mass Mortality of Northern Bay Scallops, *Argopecten irradians irradians*, Following a Severe Spring Rainstorm¹

by

STEPHEN T. TETTELBACH, PETER J. AUSTER,

The University of Connecticut, Marine Sciences Institute, Marine Research Laboratory, Noank, Connecticut 06340

EDWIN W. RHODES, AND JAMES C. WIDMAN

National Marine Fisheries Service, Northeast Fisheries Center, NOAA, Milford, Connecticut 06460

Abstract. Observations of a mass mortality of northern bay scallops, *Argopecten irradians irradians*, were made shortly after a severe rainstorm on 5-6 June 1982 during which more than 21 cm of rain fell on the Poquonock River area in Groton, Connecticut, USA. Mortality levels approached 100% at locations highest in the estuary, and decreased with distance from the head, and with depth. Observed levels of bay scallop mortality resulting from estimated periods of exposure to reduced salinities compared well with published laboratory determinations. All other lines of evidence also support the conclusion that the bay scallop mass mortality resulted directly from low salinities incurred by the storm.

INTRODUCTION

THE EFFECTS OF salinity reductions on estuarine fauna depend on the nature of the morphological, physiological, and behavioral attributes that particular species possess for coping with changes in salinity (see KINNE, 1964, for general review). Most bivalve mollusks are especially susceptible to salinity fluctuations because of their limited mobility and virtual inability to osmoregulate over wide ranges of salinity (GILLES, 1975).

As epibenthic estuarine inhabitants, bay scallops may suffer considerable exposure to freshets in the natural environment (BROOM, 1976). GUTSELL (1930) reported mortalities of *Argopecten irradians concentricus* in North Carolina that were apparently related to reduced salinities and suggested that freshets may be extremely destructive to natural bay scallop populations.

In this paper, we report a mass mortality of northern bay scallops, *Argopecten irradians irradians* (Lamarck,

1819), that occurred in the Poquonock River in Groton, Connecticut following a severe rainstorm on 5-6 June 1982, during which more than 21 cm of rain was recorded (City of Groton Water Filtration Plant, unpublished data).

AREA OF STUDY

The Poquonock River is a shallow, well-flushed estuary adjoining the eastern portion of Long Island Sound (Figure 1). The mean depth of the river is 0.95 m, the average tidal range is 0.79 m, and the residual volume of the estuary at mean low water (MLW) is 945,000 m³ (2.5 × 10⁸ gals; Tettelbach, unpublished data). Although detailed salinity profiles are unavailable, Rafferty (unpublished data) reports that, during the summer, salinity levels generally range from 20 to 30‰ at the head and 26 to 35‰ toward the mouth of the river.

The major source of freshwater input to the Poquonock River is Great Brook. The flow of this stream is regulated by the City of Groton Water Filtration Plant (COGWFP), which is located about 0.5 km north of the estuary's head. Discharge over the weirs of the plant is considered to be approximately equivalent to the total volume of fresh-

¹ Contribution No. 168 of The University of Connecticut, Marine Sciences Institute, Marine Research Laboratory, Noank, Connecticut 06340.

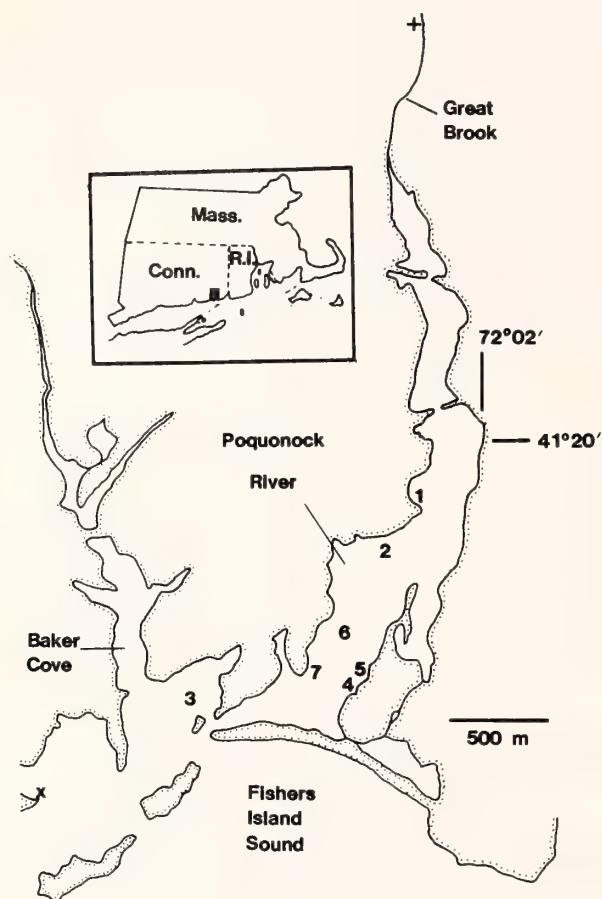


Figure 1

Map of the Poquonock River area, Groton, Connecticut, USA, with insert illustrating its location in New England. Numbers refer to sampling stations; x, location of the USGS tidal gauge; +, location of the City of Groton Water Filtration Plant.

water that enters the Poquonock River (Stevens, personal communication).

An indigenous population of northern bay scallops exists in the lower half of the estuary. Supplemental plantings of hatchery-reared scallops have been undertaken in recent years to augment the recreational fishery (STEWART *et al.*, 1981).

MATERIALS AND METHODS

Initial observations of the effects of the June 1982 rain-storm involved a qualitative survey of the scallop stocks and other estuarine fauna by biologist divers along the west side of the estuary (stations 1, 2) on 8 June 1982 (Figure 1). Water samples were collected and salinities determined by specific gravity. Tidal stage at the time of sampling was calculated in relation to values recorded at a tidal gauge (USGS, 1982, 1983) located about 1 km from the mouth of the Poquonock River (Figure 1).

On 10 June 1982, the numbers of live bay scallops and dead scallops with both valves still connected were counted *in situ* in 0.25-m² quadrats haphazardly placed in areas of known scallop concentrations (stations 3, 4). Ambient temperature and salinity measurements were taken with a Yellow Springs Instrument Co. Salinity-Conductivity-Temperature meter. On 11 June 1982, additional 0.25-m² quadrat counts were made at two depth strata (<1 m, >1 m) at station 5. Only dead scallops with all or part of the tissues remaining were counted in addition to live scallops.

Two mortality estimates were computed based on quadrat counts of live and dead bay scallops with intact hinges:

maximum mortality (%)

$$= \left(1 - \frac{\text{no. of live scallops}}{\text{no. of live scallops} + \text{no. of dead scallops (with or without tissue)}} \right) \times 100;$$

minimum mortality (%)

$$= \left(1 - \frac{\text{no. of live scallops}}{\text{no. of live scallops} + \text{no. of dead scallops (with tissue)}} \right) \times 100$$

Further observations of bay scallop mortality were made at station 6 on 17 June 1982 when pearl nets (34 × 34 × 28 cm high pyramidal nets constructed of plastic-coated wire and plastic mesh) containing hatchery-reared juveniles were examined. The nets were put in place on 27 May 1982: stocking density was 50 scallops/net (=550/m²); mean length of the scallops was 4.7 mm. Mesh size of the nets was 2–3 mm, a size that effectively excluded all predators.

In order to compare conditions in the estuary and the status of bay scallop stocks following a less severe storm than that which occurred on 5–6 June 1982, observations were made at station 7 one and four days after a storm on 10 April 1983 during which 7.8 cm of rain was recorded (COGWFP, unpublished data). Temperature and salinity measurements were made in addition to qualitative surveys of the bay scallop population.

RESULTS

Bay scallop mortality estimates and measurements of environmental parameters made at each station in the Poquonock River on the given dates are summarized in Table 1.

Initial observations made on 8 June 1982 along the western side of the Poquonock River (stations 1, 2, Figure 2) revealed that 100% of the bay scallops encountered (40–50 individuals) were dead. All were gaping widely; tissues were flaccid and runny, and showed no or only slight evidence of mechanical damage from scavengers (see Fig-

Table 1

Summary of bay scallop mortality estimates and parameter measurements acquired at the Poquonock River sampling stations following the 5–6 June 1982 rainstorm.

Station no.*	Water depth (m)	Bottom salinity (‰)	Bottom temperature (°C)	Estimated bay scallop mortality (%)	Time of sampling (h) (+) after high tide (–) before high tide	Sampling date (1982)
1	1	2.6	—	100	+2.5	June 8
2	1	3.7	—	100	+4.0	June 8
6	1	—	—	100	—	June 17
5	0.50–1.0	—	—	90.5 (min.)	—	June 11
	1.0–1.5	—	—	67.7 (min.)	—	June 11
4	0.75–1.5	14.8	16.5	91.3 (max.)	–1.75	June 10
				86.2 (min.)		
3	1	13.5	16.5	48.0 (max.)	–2.25	June 10
				0–5 (min.)		

* Stations are listed in order of increasing distance from the head of the estuary.

ures 2A, B). Other dead and dying animals in this area included juvenile winter flounder (*Pseudopleuronectes americanus*), cockles (*Laevicardium mornoni*), and sea cucumbers (*Sclerodactyla* [= *Thyone*] *briareus*), the latter being greatly bloated. Green crabs, *Carcinus maenas*, were common and active; no moribund individuals were observed.

Counts from the 12 0.25-m² quadrats made on 10 June 1982 at station 3 yielded 29 live and 27 dead scallops. All of the dead individuals seen completely lacked tissue, except for three scallops that were observed outside the quadrats. Based on these counts, the estimate of maximum bay scallop mortality at station 3 was computed to be 48%, while the minimum estimate was 0–5%.

The 12 quadrat samples taken at station 4 on 10 June 1982 yielded the following totals: 8 live and 50 dead scallops. Virtually all of the dead individuals still had part or all of the viscera present inside the shell. The minimum estimate of mortality at this location was 86.2%, while maximum mortality was calculated to be 91.3%.

Quadrat counts made at station 5 on 11 June 1982 were as follows: 0.75–1 m depth—15 live, 124 dead scallops in 20 0.25-m² quadrats; 1–1.5 m depth—31 live, 65 dead scallops in 20 0.25-m² quadrats. Estimates of minimum mortality for these two depth strata were calculated to be 90.5% and 67.7% respectively. The composite mortality estimate for station 5 was 80.4%, which was close to the estimated minimum mortality for nearby station 4 (86.2%) where depth strata were not differentiated.

The hatchery-reared juvenile bay scallops that were being held in pearl nets at station 6 were all found dead on 17 June 1982.

Observations made on 11 and 14 April 1983 in an area of bay scallop concentration (station 7) revealed that all scallops exhibited normal behavior, with velar tentacles extended, and immediately closed their valves when disturbed. Temperature and salinity measurements taken just above the sediment surface on 11 and 14 April were 9.0°C,

25.7‰, and 11.0°C, 11‰ respectively. There was no evidence of mortality resulting from reduced salinity.

DISCUSSION

On the basis of the observations described above, it seems extremely likely that the mass mortality of northern bay scallops that occurred in the Poquonock River immediately following the severe rainstorm of 5–6 June 1982 resulted from reduced salinity, as opposed to any other factor such as predation, disease, siltation, or exposure to toxic materials. The presence of large numbers of dead bay scallops with intact tissues, higher survivorship of scallops in deeper strata, and decreasing scallop mortality levels at points farther from the head of the estuary all support the above conclusion. Supplemental evidence also comes from the fact that the survival rate of scallops planted in pearl nets at station 6 two weeks after the 5–6 June rainstorm was 95% for the period July–October (Rhodes and Widman, unpublished data).

Based on the salinities recorded in the vicinity of stations 1 and 2 on 8 June 1982 (see Table 1), it appears that this area of the river may have been subjected to salinities of 4‰ or lower for as much as 48 h (and probably longer) after the storm ended. It is assumed that salinities had dropped to near these levels by the time the storm was over.

If the above assumptions are valid, then the observed mortalities of bay scallops due to exposure to these reduced salinities are consistent with laboratory results obtained by MERCALDO & RHODES (1982). These authors found that after 6 h exposure to salinities of 0 and 5‰ at temperatures of 13 and 19°C, juvenile northern bay scallops suffered no mortality; but all were dead after 24 h. When exposed to a salinity of 10‰ at these temperatures, scallops suffered 100% mortality after 48 h.

SANDERS *et al.* (1965) stated that the magnitude and



A

B



C



duration of salinity fluctuations are influenced by the size, volume, and depth of an estuary, by tidal amplitude, and by the amount (and rate) of freshwater runoff. Although such factors are important in affecting the extent to which organisms are stressed by periods of salinity reduction due to rainstorms and/or riverine discharge, it is also evident that the timing of a storm event is extremely important. As is apparent from the results obtained by MERCALDO & RHODES (1982), survival of bay scallops at low salinities is greater at lower temperatures. Therefore, storm events leading to reduced salinities may be more harmful in warmer months of the year when metabolic demands of estuarine organisms are likely to be greater.

Observations following the rainstorm of 10 April 1983 revealed that although a large amount of precipitation was recorded (7.8 cm), the volume of freshwater entering the Poquonock River, 15 million gallons/day (mgd), represented but 6% of the residual volume of the Poquonock River at MLW. Resultant salinity reductions were apparently not severe enough to directly cause any bay scallop mortality. In contrast to this, an average of 250 mgd overflowed the weirs of the COGWFP during the period 6–8 June 1982, representing a daily input equal to the residual volume of the Poquonock River at MLW. This inundation of the Poquonock River resulted in the drastic reduction in salinities and the subsequent mass mortality of bay scallops.

Under the most extreme conditions, reduced salinities resulting from storm events may contribute to the local extinction of certain populations of estuarine invertebrates. ANDREWS (1973) reported that many estuarine species of sponges, tunicates, echinoderms, and mollusks were eliminated from portions of Chesapeake Bay following tropical storm Agnes in June 1972. Although rainstorms as severe as that of 5–6 June 1982 in the Poquonock River and that of June 1972 in Chesapeake Bay may occur only once every several hundred years at a specific locality, such events may be seen as important recurring processes that can cause mass mortalities of certain invertebrate species.

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Figure 2

Dead northern bay scallops, *Argopecten irradians irradians*, photographed four days after the 5–6 June 1982 rainstorm in the Poquonock River. Note the flaccid tissue remains, some of which are being fed on by scavengers: the grass shrimp *Palaemonetes* sp. (A) and the mud snail *Ilyanassa obsoleta* (B). Scavengers initially fed mostly on scallop viscera, leaving the adductor muscle intact (C).

Shell Growth, Trauma, and Repair as an Indicator of Life History for *Nautilus*

by

JOHN M. ARNOLD

Kewalo Marine Laboratory, Pacific Biomedical Research Center,
University of Hawaii, Honolulu, Hawaii 96813

Abstract. By examining the shells of *Nautilus pompilius*, it has been possible to partially reconstruct the life history of individual animals. Two types of predation were found: (1) boreholes apparently made by an octopod and most frequently occurring over the left retractor muscle and (2) spalls or triangular notches apparently caused by *Nautilus* attacking other *Nautilus*. This intraspecific predation (cannibalism) can be divided into: (1) nips—incomplete penetration of the edges of the shell, (2) bites—removal of beak-sized and shaped pieces of shell, and (3) crunches—removal of large amounts of shell and mantle. Other types of mechanical damage may remove as much as one-quarter of the shell of the living chamber and the animal recovers and secretes new shell with an interruption in shell pattern. Foreign substances in the wound area or damage to the mantle resulted in abnormal shell deposition. Abnormal growth patterns and lumps were frequently observed. Some of these were caused by commensal organisms but others are of unknown etiology. Shell growths were found which appeared to have been caused by tumors of the mantle.

INTRODUCTION

ATTEMPTS TO STUDY the biology of lesser known animals are frequently frustrated by the very reason for which they are not better known: they are either extremely rare or live in inaccessible places. Although *Nautilus* has great intrinsic interests as the last living remnant of a large and once important marine class (HOUSE & SENIOR, 1981), it remains poorly known because of its remote habitat. Paradoxically, this remote, precise, and stable environment has allowed *Nautilus* to retain its primitive nature. *Nautilus pompilius* is a benthic animal which migrates nocturnally from depths as great as 700 m (HAVEN, 1972; SAUNDERS & WEHMAN, 1977) to depths of about 100 to 150 m where it feeds. Even at 100 m, these animals are below the workable range of scuba divers. There are two possible means of study: removal to an artificial environment and use of indirect evidence to gain insight into the life history of *Nautilus*. The latter approach is the subject of this study.

MATERIALS AND METHODS

This study was carried out on material collected mainly in October and November 1979 during the last cruise of

the R/V *Alpha Helix*. Living specimens of *Nautilus pompilius* were purchased from local fishermen who captured them in split bamboo traps made for the purpose. These traps were set usually at depths of approximately 150 m but each group of fishermen seemed to have favorite depths and locations in the Tañon Strait between the islands of Negros and Cebu (123.2°E, 10°N). Although a variety of different baits was tried, including several varieties of fish, squid, piglets, and puppies, the consensus of the local fishermen was that freshly killed chicken was most effective. Between 12 October and 20 November 1979, 332 adult and juvenile animals were collected and examined and those showing interesting shell abnormalities or damage were reserved for further study. Selection was subjective because of the contingencies of shipboard conditions but tended to be consistent because specific criteria were used. All the animals captured were weighed, sexed if possible, serially numbered, and then held in running seawater (10–15°C) for variable periods of time; then the shells were examined in detail. Some animals were maintained for as long as six weeks in apparent good health.

Shells of living animals that showed repaired damage or other abnormalities were examined to determine if the damage was related to capture and subsequent handling

or if it had occurred naturally. Damage associated with recent collection was easy to eliminate because of the newness of the fracture or damage to soft tissues.

Fishermen, shell dealers, and children frequently offered empty *Nautilus pompilius* shells for sale. These shells were also examined for anomalies. Most of these shells were "beach" or "drift" shells which showed evidence of having been dead for some time before collection. Bored shells were included for study. Purchased shells were designated with the prefix "P" followed by a number.

Included in this study are three abnormal shells recently named *Nautilus belauensis* Saunders, 1981, from Palau which were kept in the Waikiki Aquarium for varying lengths of time. They are designated with the prefix "W." The conditions of capture and maintenance are described by CARLSON (1979). The author retains all of these shells for further study.

RESULTS

The types of shell abnormalities that reflect the life history of the individual are categorized as follows: (1) Mechanical alteration of the shell resulting from (a) predatory damage, and (b) repair of mechanical and/or predatory damage. (2) Growth alterations caused by (a) imperfect repair and regrowth, (b) interference by commensal organisms, (c) abnormal and tumorous growth, (d) artificial maintenance, and (e) irregular size change.

Mechanical Alterations

Predatory damage: *Nautilus* shells show two types of damage related to presumed predation: bored holes and bites from the shell. Boreholes in or near the terminal chamber are apparently caused by another mollusk, possibly an octopod. In 1982 I saw a trap set in the Tañon Strait that contained six living *Nautilus pompilius*, one dead *N. pompilius*, and a mature male *Octopus cyanea*. The dead *Nautilus* had a borehole in the shell over the left retractor muscle and a portion of the body had been eaten. The local fishermen who set the trap said this was a common occurrence. These boreholes are ovate to diamond-shaped (Figure 1) and show striations on the side wall. They are subconical in shape and narrowest at the inner peak end. Shape and size are suggestive of the holes produced in *Strombus* and other shells by *Octopus vulgaris* (PILSON & TAYLOR, 1961; ARNOLD & OKERLUND-ARNOLD, 1969; WODINSKY, 1969; NIXON *et al.*, 1980) and in *Nautilus* (TUCKER & MAPES, 1978). Fifteen such boreholes were found in 348 shells (collected and purchased), with one shell having three holes, two having two holes each, and all other shells with one hole each. In 10 of 15 instances, the boreholes were located over the left retractor muscle, and the point of penetration continued through the conchiolin-like layer separating the muscle from the shell and to the muscle tissue itself (Figure 1b).

When the borehole was not over the left retractor, the

animal was either given to us live, or reportedly was still alive when taken by the donor. In shell P1, three holes were bored: two were on the right side of the living chamber 8.0 and 8.8 cm from the lip, and the third hole was about 7 mm inside the lower edge of the left retractor muscle. Shell P2 had two completed holes near the midline, one was 6 cm back from the lip and the other was 8.1 cm back and 1.3 cm left of the midline. This animal was in the early stages of forming a new septum. Shell P5 was acquired freshly dead with shreds of drying retractor muscle in place. There was one completed hole 9 cm back from the shell lip 1.2 cm to the right of the midline, and a second hole was over the retractor muscle scar at least 2 cm from the outermost edge.

The second evidence of predation was obtained by direct observation of captive animals. It was frequently noted that one *Nautilus* would grip another so the shell apertures were opposed and the beak of one animal attacked the lip of the shell of the other animal. Pieces of shell could be seen and heard to be broken away in these encounters, which lasted from minutes to several hours (see also WARD & WICKSTEN, 1980). Damage varied in severity and was of three types: nips, bites, and crunches.

Nips are here defined as point breaks through the outer layer of shell (called porcelainous ostracum by STENZEL [1964]) to the pearly underlying nacreous layer (Figure 2). When freshly produced (*i.e.*, witnessed), these nips are usually within 6 mm of the edge of the shell lip and tend to be oblong and vary in width from 1.2 to 1.5 mm. The bottom of these nips is usually flat. On some occasions the nips penetrate through the shell and are subsequently sealed with a layer of black organic film as described by STENZEL (1964). The nips do not have the characteristic diamond shape and striations of boreholes, and frequently have "shelves" and "plateaus" suggestive of spalls parallel to the surface of the layers. Occasionally several nips coalesce forming a large area of exposed nacre. Occasionally nips could be seen some distance back from the current shell edge indicating subsequent growth had occurred.

Bites are defined as triangular beak-shaped pieces removed from the shell at the edge of the aperture. Bites vary in size depending on how deeply the shell edge was drawn into the jaws. Frequently, they occur in connected linear arrays (Figure 3). On occasion, these arrays extended for several centimeters along the lip of the shell and when combined make deep curved or scalloped indentations (Figure 4) which may be several square centimeters in area (Figure 6). Frequently, cracks that originate at the bite coalesce and remove portions of the shell (see crunches below). Cracks often approximate or parallel the direction of the midline, then suddenly curve off sharply toward one side (Figure 5). This type of break can be easily duplicated by pressure applied to the shell surface with a pair of narrow pliers or, less easily made, by a sharp blow at the lip of a submerged shell. The curved part of the break almost invariably has evenly spaced (harmonic?) chipping along its outer surface. In

12 of 16 shells of females, this excision occurs on the animal's left side.

Crunches are here defined as large areas of missing shell (*i.e.*, several times larger than the beak area). These may result either from the coalescence of several bites into a common break or from the intersection of cracks. Possibly some of these large "crunches" are the result of mechanical damage caused by accidental contact with hard surfaces or even by attacks by larger unknown animals (*e.g.*, possibly by turtles, LEHMANN, 1981), but because of the association of the easily identifiable bites near the crunches, it appears that at least some are caused by fractures related to the bites (Figure 6). The mechanical damage and large areas of damage resulting from bites or other unknown factors will be considered together for purposes of discussion.

Repair of mechanical and/or predatory damage: Almost every shell examined in this study showed some evidence of repaired predation or other damage. The degree of repair and retention of the original shell proportions varied with the extent of shell and underlying mantle tissue damage. If the mantle was extensively damaged (*e.g.*, by attack from another *Nautilus*), the shell was frequently

imperfectly repaired and subsequent outgrowth was abnormal. The effect on the shell varied from interruption of the striped color pattern to discoloration of the junction of new and old shell to extensive rough-ribbed irregular areas covered with layer(s) of black organic material (Figure 7). The damaged mantle sometimes apparently gradually recovered during regrowth and the distal shell again became smooth (Figures 5, 8). However, in other cases the damaged mantle continued to lay down abnormal shell, and the width of the longitudinal stripes enlarged in proportion to the expansion of the shell diameter (Figure 7). It was not possible to derive an exact estimate of the percentage of shells with repaired breaks because early damage is covered by subsequent whorls and some later damage is repaired, but of the 332 shells examined in the 1979 collection only a few animals (less than 2%) were judged to be unflawed by breakage at some time in their life span. Because of shipboard limitations, it was not possible to determine experimentally how much of the shell could be removed without causing death of the animal but, judging from repaired natural breaks (*e.g.*, Figure 9), at least one-quarter of the shell could be missing and eventually replaced. There was no way of estimating the amount of soft tissue that could be lost, but Figure 10 shows an

Explanation of Figures 1 to 12

Figure 1a, b. a. Position of the borehole over the left retractor muscle. Note also that this shell had serpulid tubes near the lip and the barnacle basal plate near the umbilicus (*cf.* Figure 24). b. Higher magnification of the borehole shows it to resemble strongly those found drilled in *Strombus* shells by *Octopus vulgaris*.

Figure 2. "Nips" at the edge of the shell. These are shallow depressions which occasionally penetrate the shell. Penetrations become plugged with a layer of black organic material (broad arrow) (shell 363).

Figure 3a, b. a. "Bites" witnessed being taken by aquarium specimens in the shell of *Nautilus*. b. Bites on the edge of the shell of a collected specimen. These bites are the size and shape of the adult beak. There is also a repaired "crunch" on the left of the midline (arrow) (shell 441).

Figure 4. Damage from repeated bites on the shell. This animal has obviously been attacked frequently and the mantle was damaged at the midline so that it secreted abnormal ribbed shell. The mantle damage on the left side eventually was overcome and normal shell was again produced (shell 489).

Figure 5. Break and loss of shell probably due to joined cracks resulting either from a bite or from mechanical damage to the shell. The curved portion of the break has harmonic chipping all along the edge. Note the abnormal shell outgrowth (arrow) which resulted from mantle damage. This suggests the break may have originated from cracks due to bites.

Figure 6. Crunches are caused either by environmental damage or by coalescence of several bites into a common large break. There is a tendency for these crunches to be on the left side of

the females which is where the beak of the male would make easiest contact during copulation. The arrows indicate abnormal shell outgrowth probably caused by mantle damage that eventually regenerated (shell 576).

Figure 7. Abnormal outgrowth after damage to the mantle. Black organic material is laid down upon normal shell and the shell is deeply ridged. This black material may be subsequently lost resulting in longitudinal striations of the shell (shell 449).

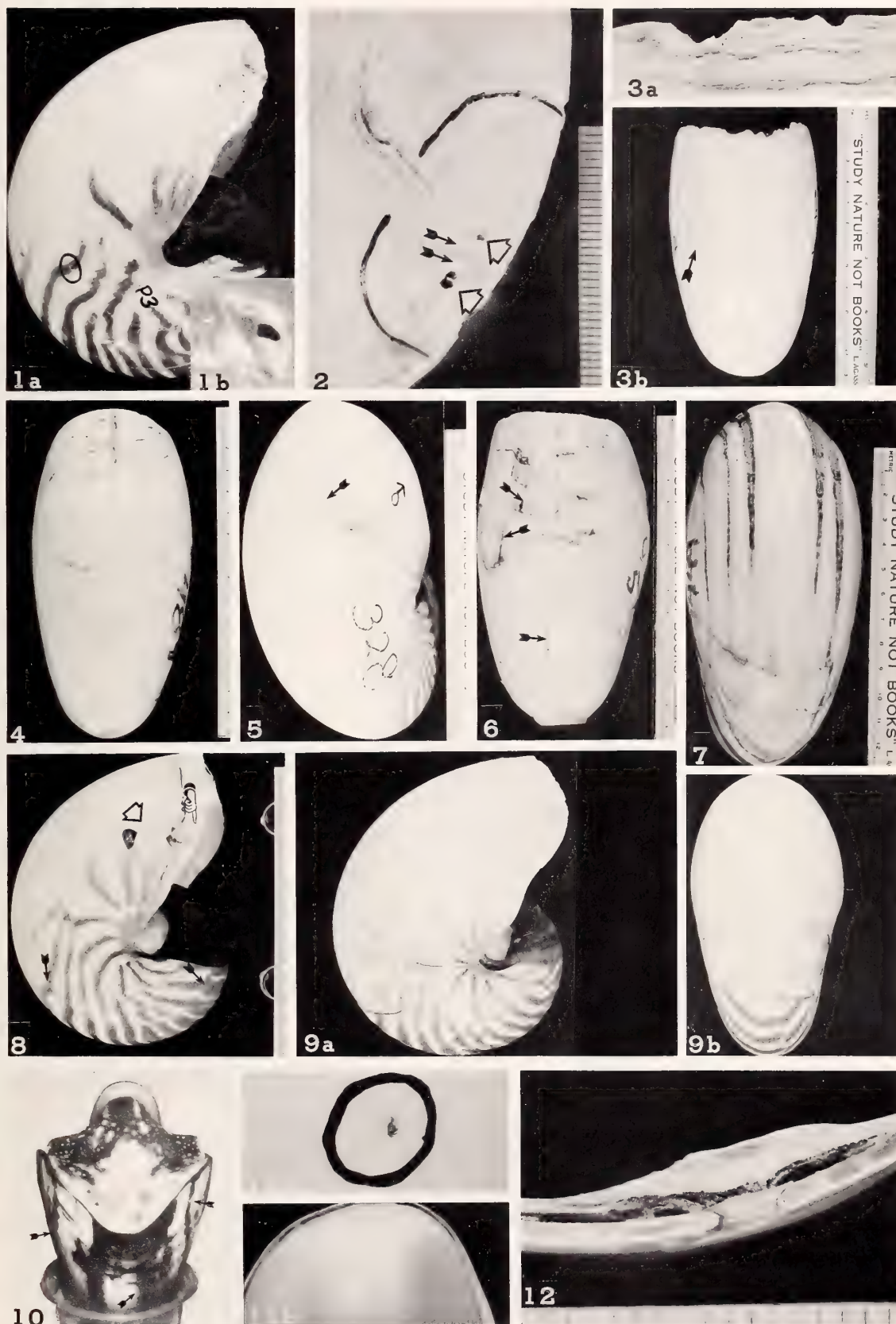
Figure 8. Abnormal outgrowth and repair of the shell as well as recovery of the mantle tissue (narrow arrow). At the broad arrow a large area of shell was cracked and elevated. The mantle then laid down an internal patch that was connected to the old outer shell by black organic material and small spheres of shell. Subsequent repair to damage along the black line resulted in a single layer of shell being formed. Note the bites evident at the black line and the recovery of mantle damage (pointer) near the lip (shell P11).

Figure 9a, b. An extensive area of shell was replaced and the stripe pattern was not resumed in the new shell (shell 182).

Figure 10. About one-quarter of the hood has been bitten off on this specimen and extensive damage to the shell was evident (arrows). Several severed arms and the buccal mass are evident and are apparently in active regeneration (shell 357).

Figure 11a, b. Patched area of shell penetration. In "a" the circle approximates the area of the internal patch. In "b" the patch can be seen to be composed of several layers of shell (shell 332).

Figure 12. Section of the patched region of shell 332. A space exists between the old damaged shell and the newly laid patch. Black organic material covers the inside of the patch.



animal in which extensive damage to the cirri, hood, buccal mass, and shell has occurred (probably due to attack by another *Nautilus*) and regeneration was occurring.

Growth Alterations

Imperfect repair and regrowth: Completeness of damage repair was proportional to the severity of damage. Where the shell was not completely penetrated by a nip, there was usually no repair, or at most a thin layer of non-reflective white material was laid down inside the shell. Where the shell had been penetrated, a pearly material was laid down upon the organic black material. Figures 11a and b show the outside and inside of a shell apparently partially penetrated by a sharp object (perhaps the lower jaw of the beak). The shell at the exact point of impact was partially crushed and fragments remained in the area. The mantle laid down several concentric layers of shell inside the point of penetration, building up a total thickness of 2.56 mm as compared with a thickness of 1.05 mm in the unaffected area (Figure 12). In shell 312 (Figure 13), there were two points of penetration that forced pieces of shell inward. These crushed pieces were subsequently covered by a layer of black organic material and an irregular pearly layer was built up on it that completely closed both openings (Figure 13b). In its thickest area, the pearly material was 2.12 mm thick, not including the organic layer. No new shell was cemented directly upon the damaged shell, rather it was laid down upon the black organic material.

In some cases where the shell was penetrated, foreign

material accumulated between the shell and the mantle tissue that apparently altered shell deposition. In shell 438 (Figure 14) the outside of the shell was penetrated and a tunnel continued internal to the damaged area. When the animal had been freshly removed from the shell, the hole had a characteristic rank odor. This odor has been noticed in other animals with abnormal shells. There was no trace of any burrowing organism visible with a dissecting microscope before or after the shell was sectioned. The damage was apparently repaired before the proximal hole was formed, as the removed distal shell had been replaced to a thickness of approximately 1 mm. The inside of the proximal hole had an ovate opening 1.16 cm long which was surrounded by a thickened area about 4.6 mm in maximal thickness and covering approximately 37 cm². The inside and outside openings were connected by an irregularly angled opening. In section the thickened area can be seen to be made of several layers of laminar shell laid down upon sheets of black organic material and interspersed with granular, gray, amorphous, loose material (Figure 14c).

In three other instances, abnormal growths were observed in shells in the 1979 *Alpha Helix* collection. In shell P15 (Figure 15) an abnormality of unknown origin caused growth to cease at the midline. Eventually growth was retarded along the leading edge and a line of black organic material accumulated. The source of the outside line apparently was correlated with an internal abnormality within the shell itself that ended at the beginning of the external deformation. A line of irregular black organic material was found within the nacreous layer and porce-

Explanation of Figures 13 to 19

Figure 13a, b. Repair of a double penetration. There is a layer of black organic material between the old shell and the newly deposited pearly layer.

Figure 14a, b, c. Traumatic shell growth caused by an open hole into the space between the mantle and shell. There are several layers of black organic material alternating with irregular small spheres of shell and organic debris. The inner surface of the repaired shell is non-reflective and porous, and gray in color. No prismatic or columnar shell is evident and a pearly layer is absent (shell 438).

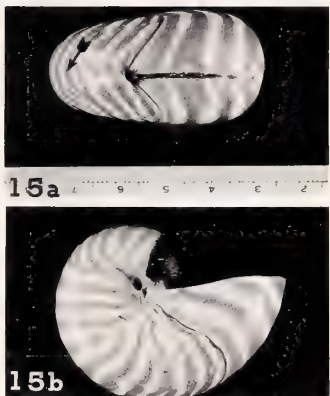
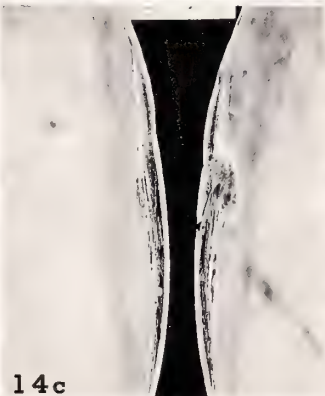
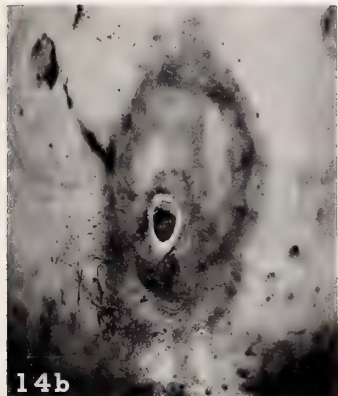
Figure 15a, b. Cessation of growth by internal shell abnormality. The arrow indicates the approximate beginning of an internal linear area of black organic material similar in appearance to the external black line. Growth ceased for a time when the abnormal shell reached the outer shell surface and a line of black material was laid down at the then distorted edge of the shell (shell P15).

Figure 16a, b. A large serpulid worm (broad arrow) in the umbilical region has inhibited outgrowth of the hood and a layer of pearly shell about 1 mm thick has been laid down (pointer). The original margin of the black organic material in the umbilical region has been retracted about 0.5 cm (arrows).

Figure 17a, b. Inhibition of growth by two serpulid worms in shell 337. In this case two small serpulid worms developed in the umbilical region (arrows indicate the ends of the worm tube). Apparently when the *Nautilus* tissues encountered the worm tubes, growth was inhibited until the worm tubes were completely covered with black organic material and some shell because a strong black line delimits the former lip and the pattern of striping is interrupted (a). This shell was sectioned (b) and it was apparent that the uniform increase in chamber size was interrupted (lc = length of the chamber in cm at the outside midline) and during this time the shell increased in thickness (wt = wall thickness at the outside midline in mm). Normal chamber size increased again and the shell regained its normal thickness; apparently then the obstructing worm tubes had been covered. For purposes of presentation the chambers are numbered in reverse order of appearance.

Figure 18. Barnacle basal plates in the umbilical region. A secondary limit of the black organic layer was developed about 3.3 mm back from the original margin (broad arrow).

Figure 19. Shell 332 with putative growth inhibition caused by coralline algae in the umbilical region (arrows).



laneous ostracum. This line began as a few black specks 1.7 cm proximal to the former shell lip, and it expanded laterally and vertically producing an elongate irregular space filled with unoriented layers of black organic material. At maximum it was 3.05 mm wide but less than 0.5 mm thick. No identifiable remnant of any substance of animal origin was found. The shell resumed growth after a period of inhibition and the color pattern was re-established. At the inner margin of the umbilicus a space 2.5×2.0 mm caused by centrifugal displacement of the distal-most chambers curved backward at least several mm (Figure 15b). Growth in volume of the chambers from the first chamber to the seventh was uniform, decreased sharply (probably due to hatching, COCHRAN *et al.*, 1981), then resumed increasing uniformly again until the thirteenth chamber which measures 6.7 mm at the outer midline as compared with 7.8 mm for the twelfth chamber and 8.0 mm for the fourteenth chamber. From the fourteenth chamber outward, the chambers increase uniformly.

Interference by commensal organisms: Many specimens of *Nautilus pompilius* had commensal organisms growing on them. Ectoprocts commonly were found in a midline patch extending from a few centimeters beyond the edge of the dorsal mantle fold to the point at which the stripe pattern ends. The ectoprocts apparently did not damage the shells. Depending on position and size, serpulid worms and at least two species of coralline algae did interfere with growth (Figures 21, 22, 23, 24). Large serpulid worms in the umbilical area seemed to cause the

most shell response (shell 338, Figure 16). At first the tube was oriented radially toward the umbilicus; then, perhaps on contact with the hood, it deviated and followed the contour of the hood. At the posterior edge of the hood, a layer of pearly shell approximately 1 mm thick and 1 cm wide was laid down upon the black organic film. Total growth was apparently retarded because the original leading edge of the black material was retracted about 0.5 cm on the umbilical region opposite the worm tube. Shell 337 shows stronger growth inhibition evidently caused by serpulid worms (Figure 17). Two worm tubes were laid down in each umbilical region when the shell was several chambers smaller than when captured. They were eventually covered with black organic material and reduced to a low ridge. The worm tubes, however, (1) inhibited growth and a black line developed at the edge of the immature lip, (2) interrupted uniform chamber growth, and (3) changed the thickness of the shell (Figure 17b). Apparently when the worm tubes were encountered, chamber growth suddenly decreased and the outer shell wall increased in thickness from less than 1 mm to 1.9 mm for the next chamber, then decreased to 1.5 mm thick in the following chamber, then resumed a thickness of 1 mm again in the next chamber. The position of the black line coincides exactly with the position of the lip at the time of worm tube interference (Figure 17a).

Growth was seemingly inhibited by barnacles at the edge of the right umbilical region of shell P3 (Figure 18). There is a secondary layer of black film 3.3 mm back from the edge of the maximum extent of the underlying black film. On shell 332 a pink coralline alga has encrust-

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Explanation of Figures 20 to 26

Figure 20a, b, c, d. Effects of a massive shell inclusion of unknown etiology upon subsequent growth of the whole animal. a. Shows there was a sharp break in the uniform volume increase (arrow) of the shell. The shell was thickened on this side. b. Shell sectioned to show the inclusion *in situ* (shell slightly tipped to facilitate visibility). The proximal portion is covered with a layer of shiny shell. c. Higher magnification of the inclusion. Three areas are evident: the hard shiny proximal area (1) is separated from a layered gray area (2) by an area of mixed black organic material and irregular spheres (3). d. Section through the inclusion showing a layer of prismatic shell (ps) proximally covering an area primarily filled with layers of black organic material upon which spherical gray shell has been laid down (bmss) followed by thin stacks of layers of whitish shell (shell 506).

Figure 21. Solid pearly inclusion in shell 303. When this lump was sectioned, it was found to be pure pearl, and no obvious irritant or growth inducing substance was evident.

Figure 22a, b, c. Shell W8 (*Nautilus belauensis*) has an open umbilicus on the right side of the shell (Figure 22c) and on the left side the umbilicus is closed (Figure 22b). Inside the left

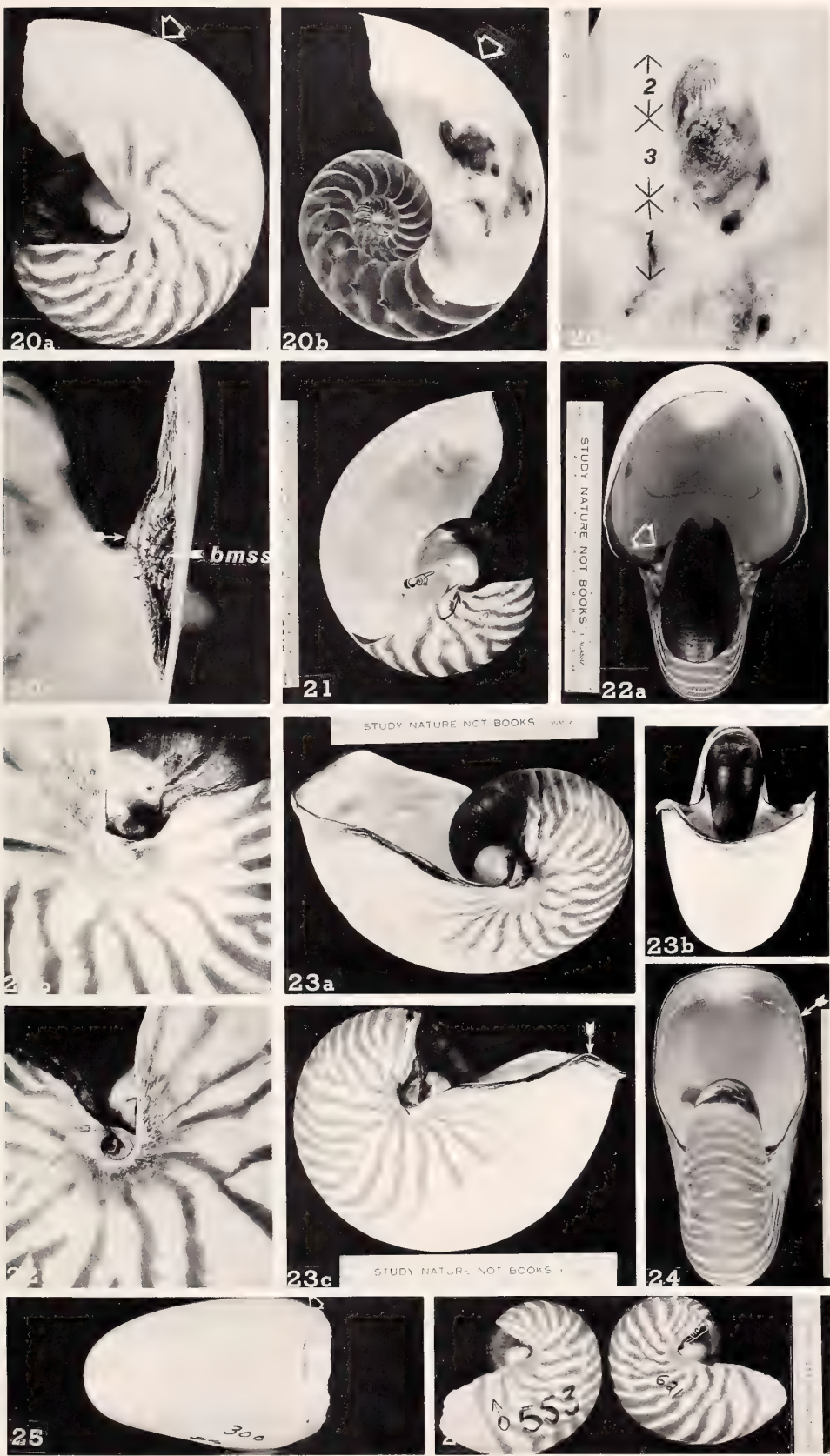
umbilicus there is a large inclusion which may possibly have interfered with shell secretion in this area (Figure 22a).

Figure 23a, b, c. Shell W9 (*Nautilus belauensis*) was kept in the Waikiki Aquarium for about 14 months during which time the shell grew abnormally outward from the lip. Note the secondary line of black organic material across the umbilicus (a, b) and the alternation of the layers of black organic material and shell (arrows).

Figure 24. The edge of shell W6 (*Nautilus belauensis*) had extra pearl laid down upon the inside of the lip. The dotted line indicated the approximate limit of the new pearly layer. The arrow indicated alternation of black organic material and white shell.

Figure 25. Shell 300 shows an abrupt decrease in the size of the living chamber for unknown reasons. It appears the relatively slight damage at the midline and right side occurred after the shell diameter had begun to decrease. There is a line of black organic material at the margin where the decrease began. This was an immature female.

Figure 26. Comparison of two juveniles taken from the same locality in the Tañon Strait. The right shell has an open umbilicus.



ed the umbilical area (Figure 19) and the nearby shell aperture. This animal appeared to be mature judging from a line of black organic material at the lip overlain by thin pearl. The posterior margin of the hood had retracted about 4.5 mm from the edge to a new layer of pearl about 1 mm thick laid upon the black film. A small empty worm tube 1.22 cm behind the leading edge of the lower aperture apparently did not inhibit growth.

Abnormal and tumorous growths: In shell 506 (Figure 20) an abnormal growth of unknown cause inside the shell affected subsequent growth of the animal. The outer third of the living chamber is decreased in size (arrow) and a dark line runs from the left umbilical region to 2.2 cm to the right of the midline. The right side of the living chamber decreases in diameter by several millimeters and the shell is thickened in the incurving region. A few bites taken near the midline and edge appear to have occurred after the chamber volume decrease. The abnormal growth extends from a thick region 12 cm back of the shell lip to about 5 cm from the lip. Distally it is covered with a thin but regular layer of pearly shell enclosing a lump 0.918 cm thick at its maximum. This layer grades into prismatic blocks that eventually grade into a thin gray layer upon a multilayered area that eventually fuses to the shell of the chamber (Figure 20d). Inside this abnormal growth the distal thickened portion is composed of thin sheets of shiny black organic material alternating with spaces crowded with spherical lusterless gray droplets. These droplets average less than 0.5 mm in diameter and tend to occur in stacks, or where exposed to the surface they form loose discontinuous sheets. Toward the mantle, the layers of gray droplets intergrade into prisms of white shell material packed together in rhombohedral columns. The prisms frequently have horizontal sheets of black organic material intersecting them. Approximately the distal 2 cm of this abnormal growth is arranged into sheets of calcareous material laid down upon the layers of black organic material which are spaced an average 0.2 mm apart. These sheets open outward so the areas between them communicate with the mantle space. The whole abnormal growth lies upon a layer of shell secreted upon the original shell (Figure 20d). There are two distinct ridges of hard thickened shell covered with clear chonchiolin which run from the edges of the growth to the columella and underlie the retractor muscles. No external wound appears associated with this internal growth which arises proximally without any evident source and tapers distally to normal appearing shell. Laterally it joins the surrounding shell with areas of brownish-black discoloration. There was no striking gross difference in the mantle when this animal was removed from its shell. In shell 303 (Figure 21), a solid lump $7.5 \times 4.5 \times 3.5$ mm projected toward the body from the inner side of the whorl opposite the attachment of the retractor muscle. When this lump was sectioned, it was found to be pure pearly shell with a

homogeneous structure. There was no indication of any irritant or substance that would have induced this growth.

Artificial maintenance: Shells of three animals recently described as *Nautilus belauensis* (SAUNDERS, 1981) were kept in the Waikiki Aquarium for various lengths of time and all showed abnormal growth. The right side of shell W8 has an open umbilicus that extends at least 2.7 cm inward (Figure 22). It is not filled with the hard callus typically found in *N. pompilius* from the Tañon Strait. The left umbilicus is covered with a layer of shell leaving a shallow depression. Immediately inside the aperture near the left umbilicus, there is an incrustation composed of black organic material, pearly shell, and dense discolored shell that projects about 7.2 mm into the living chamber. It is about 1.76 cm wide and about 1.6 cm in length. It has an irregular conical shape with an outwardly directed opening. The black organic layer on the inner whorl was asymmetrical on this animal.

Shell W9 (Figure 23) was kept in captivity for about fourteen months (CARLSON, 1979), during which time growth was asymmetrical and the shell was atypically thickened with a heavy pearly layer averaging 2.6 cm wide. In places the new shell was slightly thicker than 4.1 mm but averaged 3.5 mm thick for most of its extent. This pearl appeared to be laid down upon a thickened edge of several layers of black organic material. On the right side, the shell lip is recurved upon itself and has an irregular contour. The umbilical region has a secondary thickened layer (about 1.5 mm) of black organic material laid down on the original thin layer but back from the margin about 1.2 cm. A third specimen of *Nautilus belauensis* (W6) kept in the Waikiki Aquarium has a completely open umbilicus and also shows a layer of shiny pearl that has seemingly thickened the lip for a width of about 2.35 cm. This shell also has several irregular layers of black organic material interspersed between the shell layers at the extreme edge (Figure 24).

Irregular size changes: Occasionally there are shells that seemingly exhibit uniform shell growth until, for unknown reasons, the diameter of the outer chamber abruptly decreases in diameter (Figure 25). Sometimes these growth decreases seem to correlate with obvious shell trauma (breakage or internal growths) (Figure 16), but often the cause is not obvious. In two cases juvenile *N. pompilius* caught in the Tañon Strait did not have the umbilical region covered by shell and thereby superficially resembled *Nautilus macromphalus* (Figure 26). There was no detectable growth inside the shell similar to that in shell W8 reported above.

DISCUSSION

From the above results, it is evident that a partial history of the life of an individual *Nautilus* is laid down as the shell is secreted, repaired, or added to during the life span.

With reasonable care, it is possible to interpret this record and thereby indirectly gain insight into the environmental and, to some extent, physiological stresses encountered by *Nautilus*. The following life history events are discussed: (1) evidence of predation by known predators, (2) repair of shell damage, (3) imperfect growth and/or regrowth, (4) influence of commensal organisms, (5) anomalies of shell deposition (tumors), (6) environmental inadequacies of artificial maintenance, and (7) size changes due to unknown causes.

Predation: Two of the many possible types of predators have been tentatively identified: *Octopus* and *Nautilus*. The boreholes found in *Nautilus* shells resemble the holes bored by *Octopus* in other molluscan shells (PILSON & TAYLOR, 1961; ARNOLD & OKERLUND-ARNOLD, 1969; WODINSKY, 1969; NIXON, 1979a, b, 1980). The size, shape, and texture are similar. The rasp marks, however, may be a product more of the type of shell being drilled than a characteristic of the predator (NIXON, 1980). It is hard to imagine any animal other than *Octopus* being responsible because of the requirement of swimming by the predator and the ability of the predator to learn to position the borehole exactly over the retractor muscle (cf. ARNOLD & OKERLUND-ARNOLD, 1969). Furthermore, the presence of an *Octopus cyanea* in the same trap as a bored and partially eaten *Nautilus* is strong circumstantial evidence that *Octopus* is a predator upon *Nautilus*. In drilling *Strombus* shells, *Octopus vulgaris* consistently drills in a particular location (ARNOLD & OKERLUND-ARNOLD, 1969; WODINSKY, 1969). In *Nautilus*, holes bored in places other than over the retractor muscle were apparently unsuccessful. Living *Nautilus* specimens were captured with complete boreholes not over the muscle but shells that contained living animals were never found with completed boreholes over the muscle area. The tendency to drill on the animal's left side may possibly be due to the right-hand position of the beak of the male which would make an attacker to the right side more vulnerable to counter-attack. Therefore, there would be an advantage to learn to bore consistently over the left retractor muscle.

That *Nautilus* is preyed upon by other *Nautilus* was directly established. Almost all shells show evidence of beak-shaped bites and attacks of this type were witnessed. Frequently during copulation the male bites the shell, mantle, hood, and arms of the female in his grasp. Because of the off-center position of the spadex, the male's beak opposes the left side of the female's midline, and there is a tendency (12 of 16 cases) for the females to have more repaired crunches on the left side. The question remains whether the encounters are lethal; in the case of the animal shown in Figure 10, extensive damage was done yet regeneration was occurring. If not lethal, attacks must be detrimental because repair and regeneration require metabolic effort.

Repair of shell damage: The most striking damage in-

volved the breaking away of large areas of shell (Figures 5, 6, 9). It is not possible to identify the causes of all the large breaks but certainly some must be the result of conjoined cracks from bites. Displaced edges are frequently rejoined by a layer of black organic material which later becomes covered by shell (Figure 8). In other cases a line of new shell secretion starts proximal (posterior) to the fissure giving the impression that the mantle retracted and then began to move outward again as it secreted replacement shell. Thus, extensive areas of original shell lined with new shell are common. At the junction of the "new" and "old" shell, there may or may not be a layer of black organic material underlying the new shell.

Imperfect growth and/or regrowth: The success of regrowth of shell (replacement as opposed to repair of damaged but still present shell) seems dependent on the extent and severity of the original damage. If the mantle was damaged, subsequent secretion of new shell frequently was abnormal (Figures 7, 8, 10). Apparently the interjection of foreign substances into the wound area resulted in abnormal regrowth (Figure 14). In most instances the mantle responded to shell trauma by first covering the damaged area with black organic material which was, in turn, covered with shell. In these cases the shell apparently was of uniform density and structure unlike the abnormal (tumorous) shell seen in Figures 14 and 20.

Influence of commensal organisms: Apparently, anything that physically inhibits advance of the body will interrupt the advance of the body whorl. Objects such as worm tubes, barnacles, or even such flat encrustations as coralline algae will interrupt growth. LANDMAN (1983) also observed that barnacles would inhibit *Nautilus* shell growth. This interruption of growth results in thickening of the shell and the interruption of uniform volume increases of the chambers (Figure 17). The thickening of the shell wall suggests that despite interruptions of outgrowth of the living tissue, secretion of the shell continues at a uniform rate. Further growth apparently is dependent upon the ability of the mantle and soft tissues to overcome or cover the interfering foreign objects with hard tissue. In most instances a layer of black organic material is laid over the foreign object. Apparently, when chamber outgrowth is inhibited by a foreign object in the umbilical area, the mantle retracts slightly and begins to secrete pearl over the black layer. Once the obstruction is overgrown or in some way removed, growth resumes, leaving a record as a decrease in chamber size, thickening of the shell, a layer of black material, or a combination of these demarcations.

Anomalies of shell deposition (tumors): Examination of the growths deposited in the shell shown in Figure 20 and similar shells shows that the three normally coordinated steps of shell secretion can become disassociated. Instead of a uniform laying down of shell components upon and

among the organic matrix, the black organic material is laid down in macroscopic sheets interspersed with either prismatic masses of shell or aggregates of granular material. Obviously, this reflects the pathological state of the secreting mantle and fits the definition of tumorous growths. Unfortunately, the mantles that secreted these growths are not available for histological examination.

Environmental inadequacies of artificial maintenance:

Figures 23 and 24 illustrate two shells of animals that were held in captivity and abnormal growth occurred at the shell lip of these presumably mature animals. MARTIN *et al.* (1978) have figured similar abnormal growth in a specimen of *Nautilus macromphalus* kept in captivity. Because the animals shown in Figures 19 and 20 were kept at typical environmental temperatures, it can be assumed that temperature is not the sole factor in this abnormal growth. Possibly either the conditions of maintenance were inadequate (in the same way in New Caledonia and Hawaii, which seems unlikely) or (more likely) irritation to the shell lip and mantle caused by continued contact with the walls of the container caused abnormal growth.

Size changes due to unknown causes: The cause(s) of the decrease in diameter of the terminal chamber in some shells is an open question without the soft parts. Whether this was from the need to regenerate lost tissue, as would be the case of the animal of Figure 10, or from disease or other metabolic upset requires further study.

CONCLUSIONS

It seems possible to infer by indirect methods that *Nautilus* living in their natural deep sea environments are: (1) subjected to predation by a hole-boring animal, probably an octopod, and certainly by other *Nautilus*; (2) damaged by massive mechanical shell breakage which they are able to repair and compensate for; (3) inhibited in their growth by the presence of external commensal organisms and possibly unfavorable or physiological conditions; and (4) subject to abnormal shell growth caused either by environmental conditions or tumorlike pathologies of unknown etiology. These changes in shell morphology should also be an event in the fossil record.

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staff of the Waikiki Aquarium, particularly Mr. Bruce Carlson, provided the artificially maintained animals. The Republic of the Philippines graciously allowed the R/V *Alpha Helix* to carry out its mission in their national waters, and the National Science Foundation of the United States provided financial support (Grant #PCM 77-16269). Finally, I would like to thank the crew of the *Alpha Helix* and my many scientific colleagues who made this work possible, and the staff at Scripps Institute of Oceanography who supported this cruise.

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Records and Morphology of *Lomanotus stauberi* Clark & Goetzfried, 1976, from the Panamic Pacific

by

TERRENCE M. GOSLINER

Department of Invertebrate Zoology, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118

AND

HANS BERTSCH¹

Biological Sciences, National University, San Diego, California 92106

Abstract. Specimens of *Lomanotus stauberi* Clark & Goetzfried, 1976, were collected from the Gulf of California and Pacific coast of Baja California. Morphologically they closely resemble the type material and other specimens collected from the Atlantic coast of Florida. The material collected in this study constitutes the first record of the genus *Lomanotus* from the Pacific Ocean.

INTRODUCTION

Lomanotus stauberi was described from the Atlantic coast of Florida (CLARK & GOETZFRIED, 1976). Since then no additional records of the species have been published. Specimens from the Gulf of California and the Pacific coast of Baja California (Figure 1) represent a significant extension of known range of *L. stauberi* and the first record of the genus from the Pacific Ocean. In this paper we describe the morphology of these specimens and compare them with type material and other specimens collected from the Atlantic coast of Florida.

DESCRIPTION

Material: Paratypes—National Museum of Natural History, Washington, D.C., USNM 710760, 6 specimens, Sebastian Inlet, Florida (27°51'33"N, 80°26'45"W), 1 m depth, 26 July 1975, Kerry Clark.

California Academy of Sciences, San Francisco, CASIZ 050217, 3 specimens, Boca Ratón Inlet, Florida, 1 m depth, 1 June 1975, Terrence M. Gosliner.

California Academy of Sciences, San Francisco, CASIZ 050218, 3 specimens, 10 km S of Loreto, opposite road to

El Rincón, Gulf of California, Baja California Sur, Mexico (26°55'N, 111°20'W), 3 m depth, 14 January 1984, Terrence M. Gosliner.

California Academy of Sciences, San Francisco, CASIZ 050219, 5 specimens, S end of Isla Magdalena, 200 m inside Punta Entrada, Magdalena Bay, Baja California Sur, Mexico (24°34'N, 112°03'W), 3-4 m depth, 16 January 1984, Hans Bertsch.

External morphology: The living animals (Figure 2) range in length from 11 to 14 mm. The ground color is translucent white. The notum, head, and sides of the body are brown. Irregular darker brown lines extend the entire length of the notum. A network of opaque white lines covers much of the oral tentacles, rhinophores, branchial lobes, and notum. An opaque white spot is present at the apex of each branchial lobe.

The oral veil is semicircular in shape (Figure 4). The anterior limit of the head is often upturned when the animals are actively crawling. The anterior foot corners are short and angular. Extending from the dorsolateral portion of the head are a pair of simple, acutely pointed oral tentacles. The rhinophore sheaths possess 5-9 shallow lobes. The perfoliate rhinophores are composed of 9-12 lamellae. The notum is expanded into 22-25 branchial lobes per side. Each lobe terminates at a short digitiform

¹ Mailing address: 4444 W. Pt. Loma Blvd. #83, San Diego, California 92107.

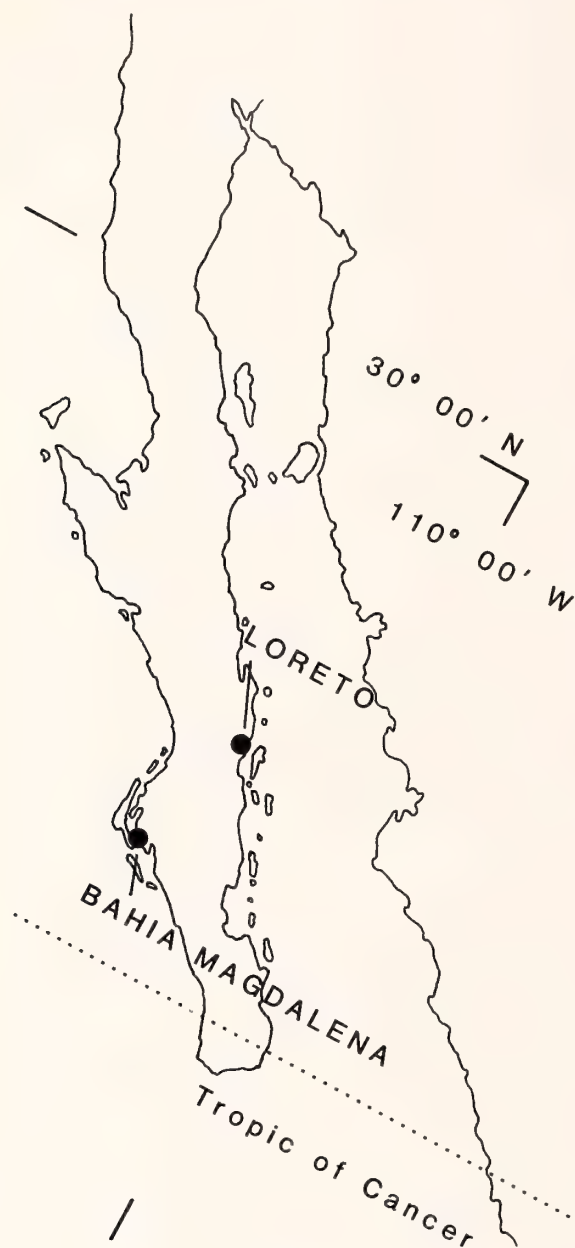


Figure 1

Map of Baja California, indicating collecting localities.

process. The genital aperture is situated ventral to the fourth and fifth branchial lobes, while the anus is located ventral to the tenth to twelfth branchial lobes.

Internal morphology: The jaws (Figure 5) possess an elongate masticatory margin that bears several rows of platelets, each of which bears 7–10 denticles (Figure 6). The radular formula is $20 \times 7-14.0.7-14$ in the single specimen examined in this study (Figures 7–11). There are 6–15 denticles on the outer side and 6–10 denticles on

the inner side of the radular teeth. The teeth are widest near the rachis of the radula and become progressively narrower near the outer margins.

The reproductive system (Figure 13) contains a narrow preampullary duct, which expands into a wider, saccate ampulla. The ampulla narrows into the postampullary duct and divides into the oviduct and vas deferens. The oviduct expands into a bilobed receptaculum seminis and narrows again where it joins the albumen, membrane and mucous glands of the female gland mass. The female glands terminate at the female aperture. The vas deferens is prostatic throughout its length and terminates at a muscular, conical penis, which is unarmed.

Egg mass: The white egg mass (Figure 3) consists of a convoluted ribbon (about 14 mm long and 2 mm across the coils) which is oriented along the longitudinal axis of the hydroid stem. Within the mass there is a single egg per capsule.

Natural history: Specimens were found on colonies of the stinging plumularid hydroid *Lytocarpus philippinus* (Kirchenpauer, 1872) in 1–4 m of water. The animals and egg masses are remarkably cryptic on the hydroid colonies. At both localities where *Lomanotus stauberi* was collected in this study, *Lytocarpus* forms dense aggregations on the tops and sides of boulders where there is slight surge.

DISCUSSION

Material collected from the Gulf of California and the Pacific coast of Mexico was compared with the original description of *Lomanotus stauberi* Clark & Goetzfried, 1976. Paratype specimens and specimens collected by one of us (TMG) from the Atlantic coast of Florida were also compared with the present material. In virtually all aspects, the morphology of the present material agrees with that known from the Atlantic coast of Florida and there is no doubt that they are conspecific.

The radula of the Pacific material contains more teeth per half row (up to 14) than that described by CLARK & GOETZFRIED (1976) where there are 7–9 teeth per half row. However, the paratype specimen examined in this study (Figure 12) contained up to 11 teeth per half row. Clark & Goetzfried also noted that specimens from Florida had as many as 31 branchial lobes per side, whereas in the present material there is a maximum of 25 per side. This is likely a function of the somewhat smaller body size of the Mexican material. These slight differences are considered minor and within the normal range of variation.

CLARK & GOETZFRIED (1976) mentioned that the penis of *Lomanotus stauberi* is conical and unarmed, but the remainder of the reproductive morphology was not described. The configuration of the reproductive organs described here is based upon the examination of three specimens, two from Isla Magdalena and one paratype from Sebastian Inlet, Florida. No morphological variability was



Explanation of Figures 2 and 3

Figure 2. *Lomanotus stauberi* Clark & Goetzfried, 1976. Living animal.

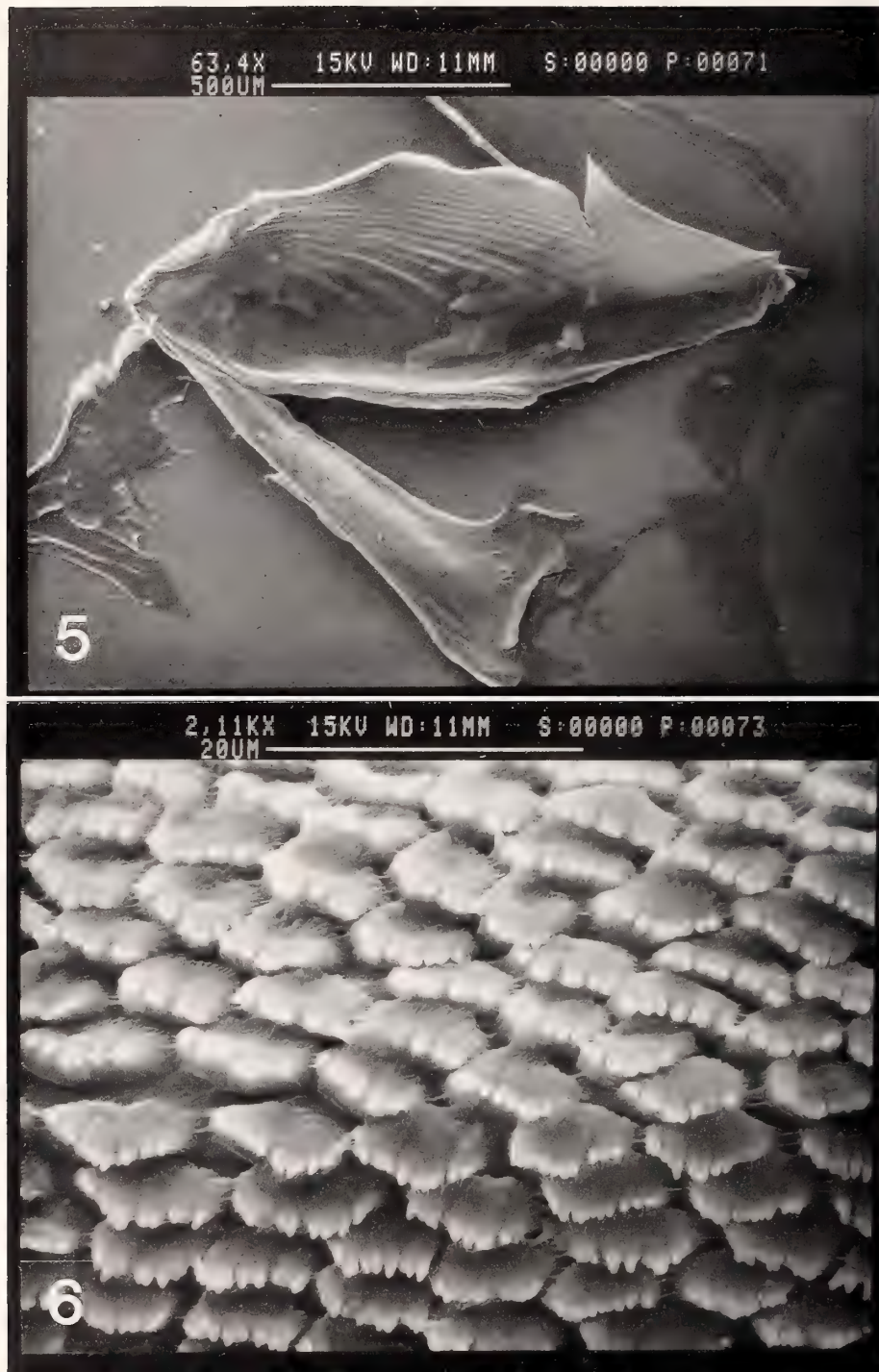
Figure 3. *Lomanotus stauberi* Clark & Goetzfried, 1976. Egg mass.

detected. The reproductive morphology of two other species of *Lomanotus* has been described. In *L. stauberi* the receptaculum seminis is bilobed while in *L. phiops* Marcus, 1957, it is undivided and in *L. genei* Verany, 1844, it is absent (see MARCUS, 1957; SCHMEKEL, 1970).

Figure 4

Lomanotus stauberi Clark & Goetzfried, 1976. Ventral view of head: f, foot; fc, foot corner; m, mouth; ot, oral tentacle. Scale = 3.0 mm.

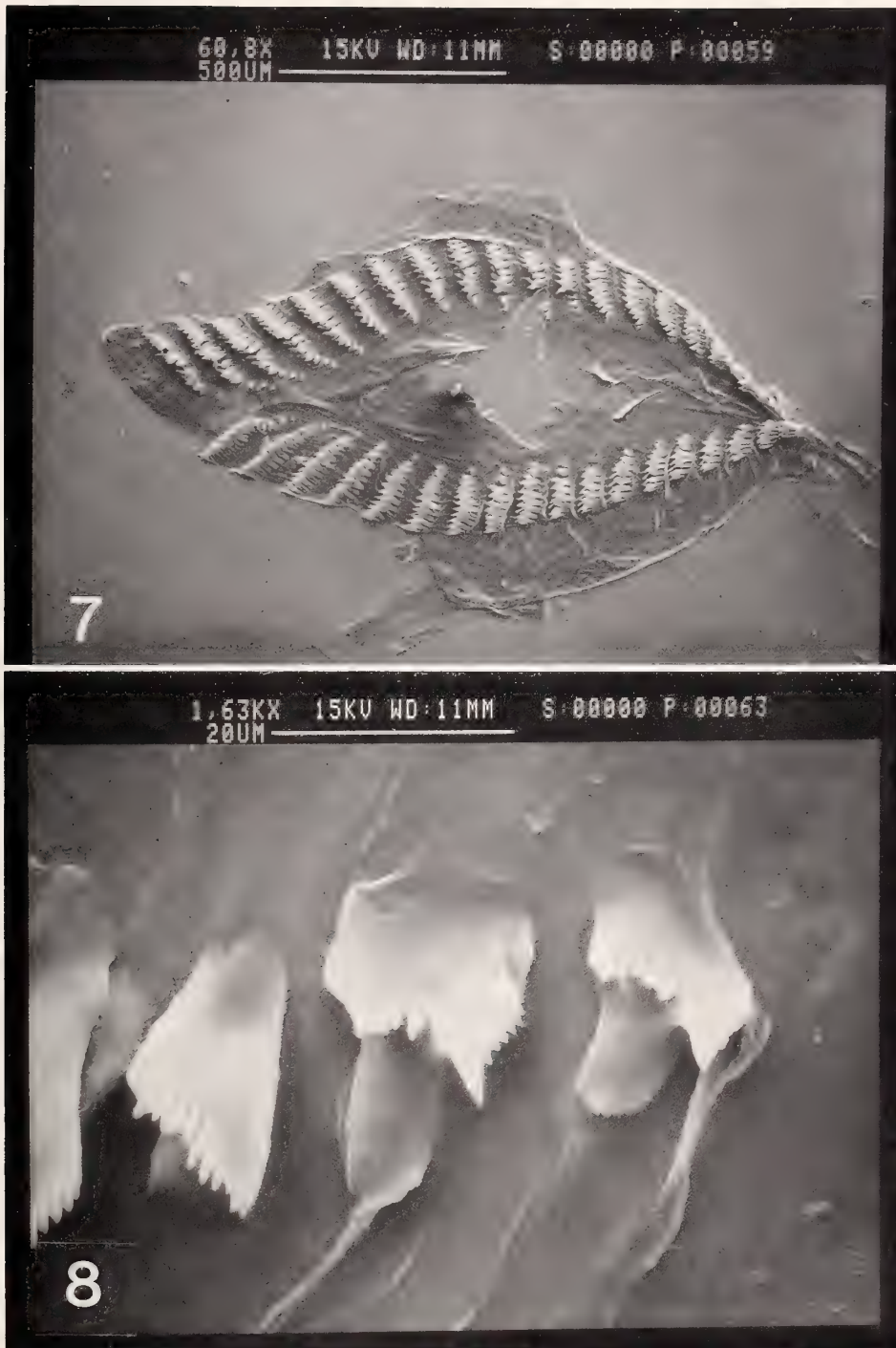




Explanation of Figures 5 and 6

Figure 5. *Lomanotus stauberi* Clark & Goetzfried, 1976. Jaw.

Figure 6. *Lomanotus stauberi* Clark & Goetzfried, 1976. Masticatory elements.



Explanation of Figures 7 and 8

Figure 7. *Lomanotus stauberi* Clark & Goetzfried, 1976. Entire radula of specimen from Loreto.

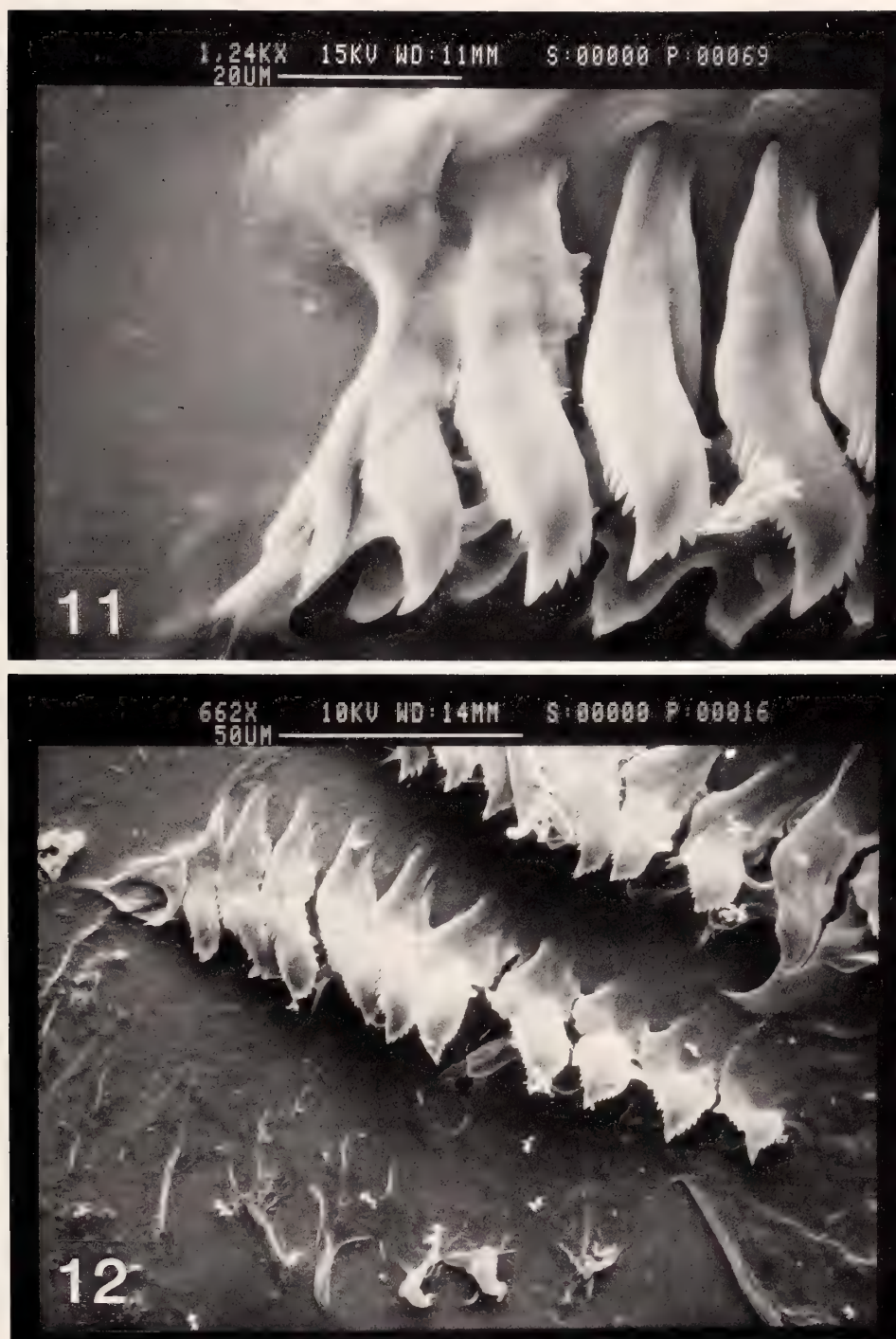
Figure 8. *Lomanotus stauberi* Clark & Goetzfried, 1976. Teeth 1-3.



Explanation of Figures 9 and 10

Figure 9. *Lomanotus stauberi* Clark & Goetzfried, 1976. Teeth 4-7.

Figure 10. *Lomanotus stauberi* Clark & Goetzfried, 1976. Teeth 7-12.



Explanation of Figures 11 and 12

Figure 11. *Lomanotus stauberi* Clark & Goetzfried, 1976. Teeth 10-14.

Figure 12. *Lomanotus stauberi* Clark & Goetzfried, 1976. Half row of radular teeth of paratype specimen.

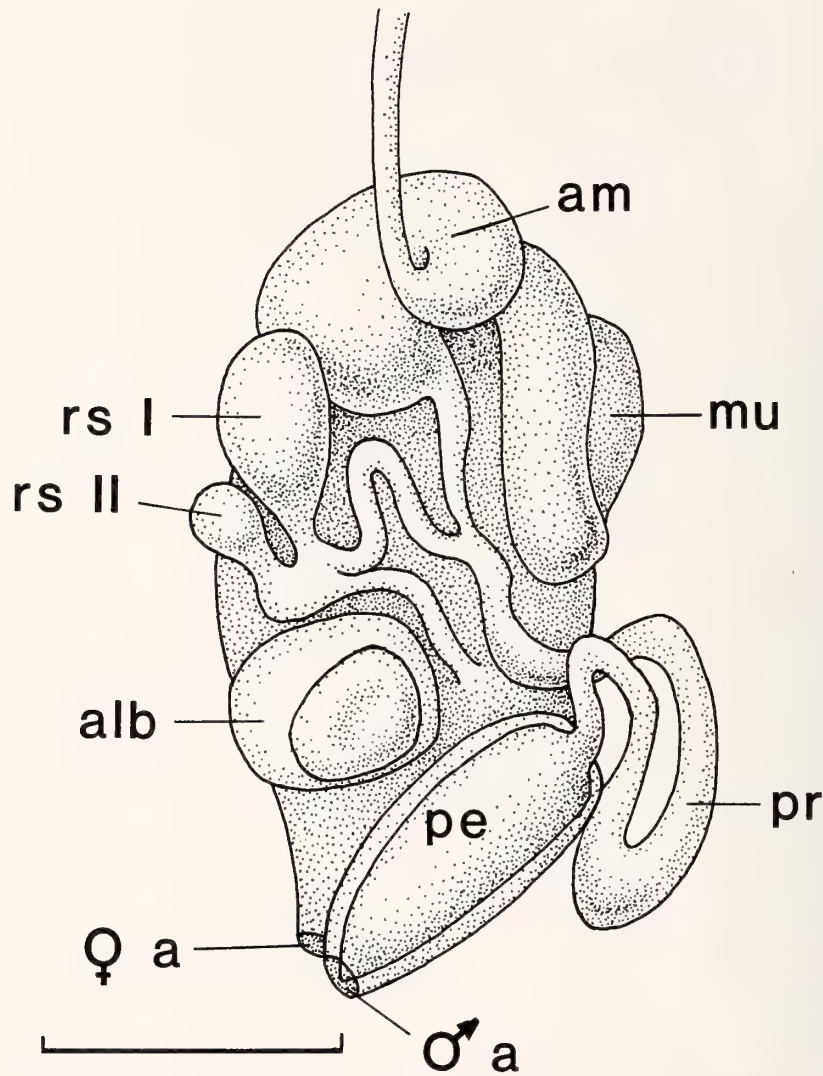


Figure 13

Lomanotus stauberi Clark & Goetzfried, 1976. Reproductive system: alb, albumen gland; am, ampulla; mu, mucous gland; pe, penis; pr, prostate; rs I, receptaculum seminis I; rs II, receptaculum seminis II; ♀a, female aperture; ♂a, male aperture. Scale = 1.0 mm.

It is difficult to make definitive judgments regarding the systematics of *Lomanotus*, as the majority of species are incompletely described. CLARK & GOETZFRIED (1976) provided a detailed review of the known morphological features of members of the genus. From their data it is clear that *L. stauberi* is most similar to *L. phiops* Marcus, 1957, and *L. vermiformis* Eliot, 1908. Clark & Goetzfried noted important radular differences between *L. stauberi* and *L. phiops*. *Lomanotus phiops* also differs from *L. stauberi* by its undulate rather than straight notal border and by its undivided rather than bilobed receptaculum seminis. It is difficult to compare *L. stauberi* with *L. vermiformis*. ELIOT (1908) described only the external morphology

and radula of *L. vermiformis* and provided no figures of his specimens. The apparent similarity of the two taxa warrants further morphological study, particularly as the prey hydroid of *L. stauberi*, *Lytocarpus philippinus* is circumtropical in its distribution (NUTTING, 1900) and is known from the Red Sea.

Lomanotus stauberi is certainly more widespread than originally indicated and has a broad distribution within the Panamic Province, having been found in the Gulf of California and on the Pacific coast of Baja California. The fact that it has not previously been encountered in the region can be attributed directly to its specialized habitat and extremely cryptic appearance when on its prey.

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Rediscovery and Redescription of *Rostanga lutescens* (Bergh, 1905), comb. nov. (Gastropoda: Nudibranchia)

by

SCOTT JOHNSON¹

Mid-Pacific Research Laboratory, Enewetak, Marshall Islands, Box 1768, APO San Francisco 96555

AND

HANS BERTSCH²

Biological Sciences, National University, San Diego, California 92106

Abstract. Living specimens of *Rostanga lutescens* (Bergh, 1905) are described for the first time. The generic position, left uncertain by Bergh, is emended, and the reproductive system and the proper arrangement of the radular teeth are described. This species is now known from Timor, Indonesia, and Enewetak Atoll.

AMONG THE opisthobranch collections of the Siboga Expedition was a single, preserved, 14 mm long dorid nudibranch, which BERGH (1905) questionably assigned to the genus *Discodoris* Bergh, 1877. Recent collections at Enewetak Atoll, Marshall Islands, west central Pacific (11°33'N, 162°20'E) have yielded three specimens essentially fitting Bergh's description; the species is here described for the first time in the living state. Voucher specimens, with mounted radulae and color slides of the living animal, have been deposited in the Bernice P. Bishop Museum (number 207564), Honolulu, Hawaii, and the United States National Museum, Washington, D.C.

The spelling of the species name needs comment. In BERGH's text (1905:107) describing the new species is printed: "*Discodoris* ? *lutesceus* Bgh. n.sp." There is no further mention of the name in the text. However, in the two indices (Inhaltsverzeichnis, p. 244; Register, p. 247), and on the explanation to plate XIV, the species is listed as *lutescens*. The single misspelling is obviously a printer's error, which Bergh himself corrected (BERGH, 1905:248, Corrigenda): "Seite 107 statt: *Disc. lutesceus*, lese man: *lutescens*."

Rostanga Bergh, 1879

Rostanga lutescens (Bergh, 1905), comb. nov.

Reference and synonymy: *Discodoris lutescens* BERGH, 1905:107-108; pl XIV, figs. 22-28.

Material examined: One specimen, 12 × 4 mm. Lagoon-side Medren Island, Enewetak Atoll, Marshall Islands; under dead coral, 5 m; 2 August 1981, *leg.* S. Johnson.

One specimen, 19 × 8 mm. Lagoonside Enewetak Island, Enewetak Atoll, Marshall Islands; under dead coral at night, 5 m; 26 February 1982, *leg.* L. Boucher.

One specimen, 15 × 6 mm. Lagoonside Enewetak Island, Enewetak Atoll, Marshall Islands; under dead coral, 5 m; 14 July 1982, *leg.* S. Johnson. This specimen, illustrated in Figure 1, has been deposited in the Malacology Department of the Bishop Museum under number 207564.

Habitat: All three specimens were collected on shallow, subtidal, lagoon reefs consisting of sand, rubble, and limestone flats in 3-6 m of water. At one time, these reefs were apparently populated by numerous colonies of the tabletop coral *Acropora hyacinthus* (Dana, 1846). Most of these colonies are long dead and lying on the bottom, with their undersides thickly overgrown with sponges, bryozoans, tunicates, and other encrusting organisms.

Description: The notum is soft and elongate-oval, and its

¹ Mailing address: P.O. Box 25702, Honolulu, Hawaii 96825.

² Mailing address: 4444 W. Pt. Loma Blvd. #83, San Diego, California 92107.

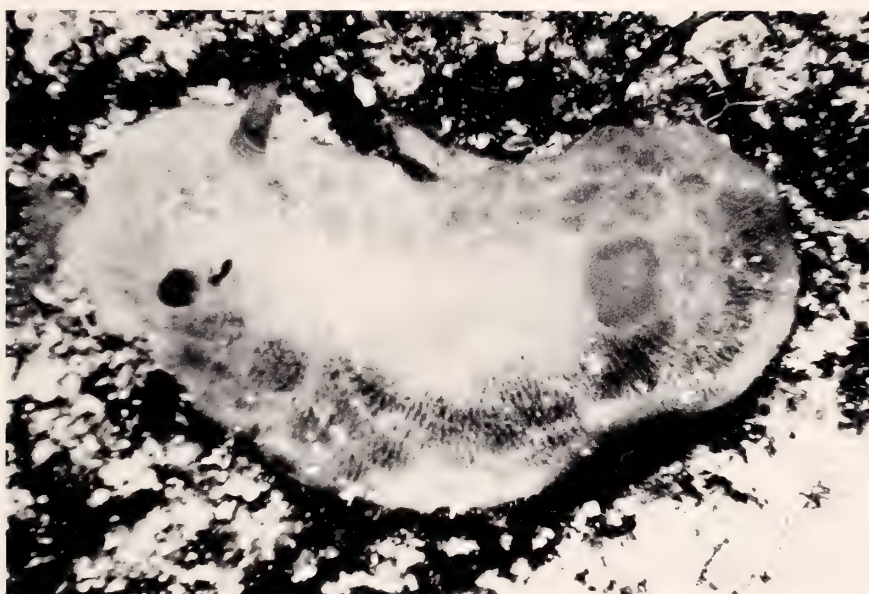


Figure 1

Photograph of living *Rostanga lutescens*, 15 × 6 mm.

wide margin hides the foot. The dorsal surface is densely crowded with fine, rounded papillae from which protrude bundles of spicules (caryophyllidia), giving the animal a hispid appearance. Notal color is light cream-yellow to light tan, usually with close-set, large, round, very slightly darker brownish spots. Irregularly scattered over the dorsal surface are small patches of opaque white. Mid-dorsally the notum appears more pinkish to orange in color, apparently because of the coloration of the underlying viscera. The underside of the overhanging hyponotum is translucent white with a white network of epidermal spicules. The foot is translucent white to pale orange, with light-orange, relatively long and slender oral tentacles. The

rhinophores, which protrude from spicule-edged pockets, have transparent stalks and yellow-brown clubs, each bearing 12–16 oblique, darker colored lamellae. Branchiae are colored as the rhinophores and consist of about 6 small, tripinnate stalks crowded together in a close circle around the anus. In ethanol, the animals become white with grayish viscera.

The radulae of the 19 and 15 mm long specimens measured 2.1×1.3 mm and 1.5×1.0 mm respectively, and the radular formulae were 56 (70.0.70) and 51 (56.0.56). The morphology of the teeth differed slightly between the two individuals. Selected teeth from a typical right half-row of the larger specimen are shown in Figure 2, and a

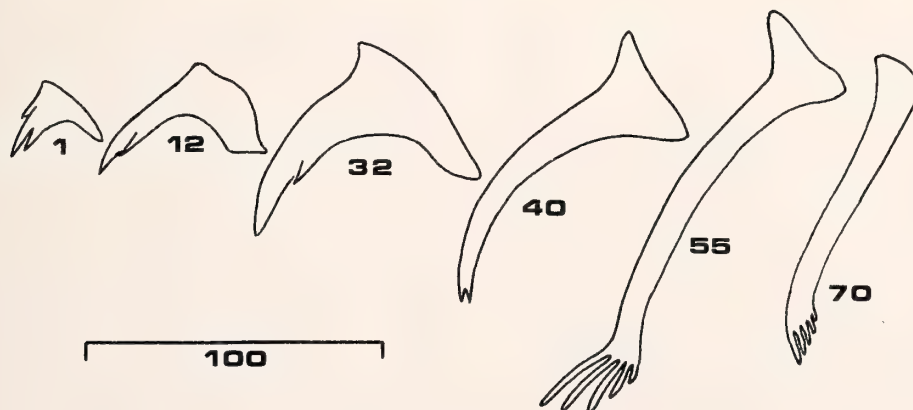


Figure 2

Rostanga lutescens, 19 mm long specimen: selected radular teeth from the right half-row. Scale bar in μm .

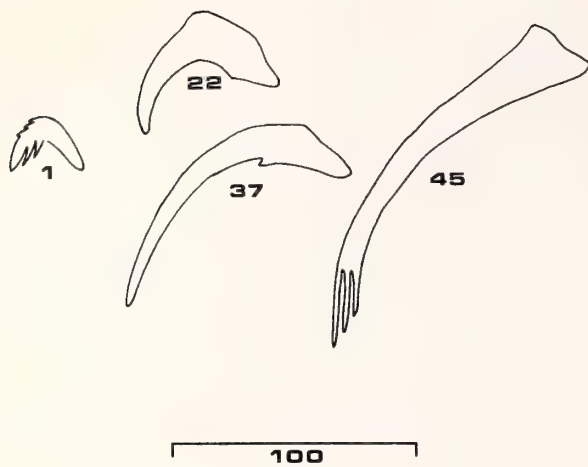


Figure 3

Rostanga lutescens, 15 mm long specimen; selected radular teeth from the right half-row. Scale bar in μm .

few of the more variant teeth from the smaller specimen in Figure 3. Generally, innermost laterals are hamate with 1 to 5 small inner denticles and 1 or 2 large outer denticles. Outwardly, teeth become larger, and denticulation may disappear by the middle of the half-row. Outer teeth are very elongate, with the tip split into as many as 5 very long, sometimes bent, fingerlike terminal spines. The outermost teeth become slightly shorter again. The long outer teeth overlap much of the radula when mounted on a slide, making details difficult to resolve. Buccal armature consists of long, slightly curved elements, which are rather bluntly pointed rods bearing ringlike, transverse thickenings (Figure 4).

The reproductive system (Figure 5) is similar to that reported for other species of *Rostanga* (compare with

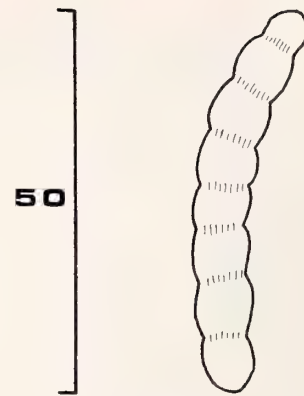


Figure 4

Rostanga lutescens; buccal element. Scale bar in μm .

SCHMEKEL & PORTMANN, 1982:text fig. 7.9 c, and plate 31, fig. 2; and MARCUS, 1958:fig. 36). A long, narrow vagina terminates in a spherical bursa copulatrix, from which an equally narrow uterine duct leads into the nidamental gland complex slightly below the ampullary and prostatic ducts. An ovate receptaculum seminis is at the end of a rather long, narrow duct budding from approximately the middle of the uterine duct. A long, curved ampulla leads into an ampullary duct that joins with the prostatic duct external to the nidamental glands. The wide, white, somewhat granular appearing prostate curls over 180° and leads into a much narrower, short penis.

Discussion: BERGH's original description (1905) mentions that there were numerous black dots along the margin of the animal. The dark spots of our animal are at times apparently composed of small darker colorations. These do not seem to be contradictory descriptions. Moreover,

Table 1

Radular characteristics and body coloration of species of *Rostanga* (modified in part from THOMPSON, 1975:490).

Species	Body color	Hamate lateral teeth	Terminal denticles of marginal teeth	Distribution
<i>R. rubra</i> (Risso, 1818)	red	first: 4 or 5 small lateral denticles following: 1 large side denticle	bifid	east Atlantic
<i>R. tenerana</i> Pruvot-Fol, 1953	—	—	bifid	east Atlantic
<i>R. evansi</i> Eliot, 1906	violet-gray	—	multifid	east Atlantic
<i>R. byga</i> Marcus, 1958	red	—	multifid	west Atlantic
<i>R. arbutus</i> (Angas, 1864)	red	first: 13 or 14 denticles	multifid	west Pacific
<i>R. muscula</i> (Abraham, 1877)	red	first: 20–30 denticles	multifid (2–4 terminal)	west Pacific
<i>R. atrata</i> (Kelaart, 1859)	black	—	multifid (10–15 terminal)	Indo-Pacific
<i>R. lutescens</i> (Bergh, 1905)	cream yellow, light tan	first: 1–5 inner denticles 1 or 2 outer following: 1 side denticle	multifid (up to 5)	west Pacific
<i>R. pulchra</i> MacFarland, 1905	red	first: 4–11 denticles	multifid	east Pacific

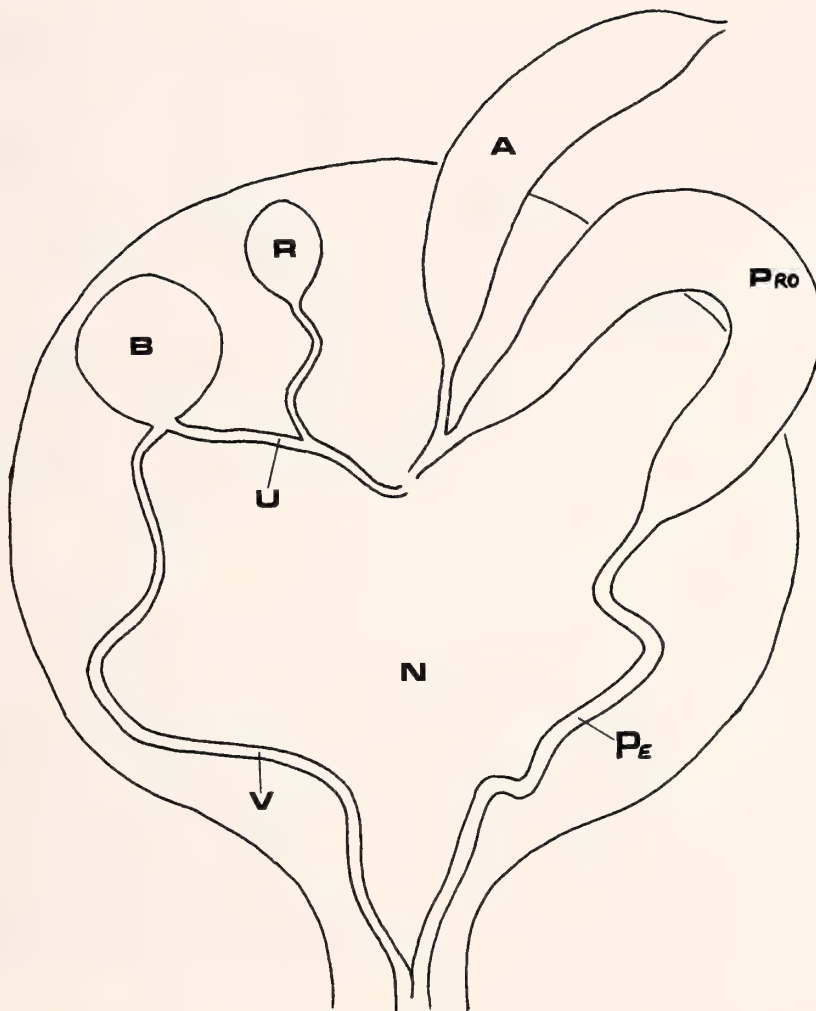


Figure 5

Rostanga lutescens; anterior genital mass. A, ampulla; B, bursa copulatrix; N, nidamental gland complex; Pe, penis; Pro, prostate; R, receptaculum seminis; U, uterine duct; V, vagina.

our specimens match his animal in general shape, size, spiculate surface, and small gills. The radular teeth of the Enewetak specimens also resemble those in Bergh's description, reproduced here in Figure 6, except for their arrangement. According to BERGH (1905), the elongate, denticulate teeth were in the middle of the half-row, and the outermost were smooth and hamate, like those from the middle of the half-row of one of the present specimens. Bergh, however, did note that he was uncertain as to how the radula was constructed: "Es glückte nicht den Bau der Raspel genauer zu bestimmen" (BERGH, 1905:108). Radulae with elongate, narrow teeth are easily jumbled, and details can be difficult to resolve. Considering Bergh's uncertainty regarding the arrangement of the elongate, denticulate teeth, it seems most likely that the correct placement of the teeth from the Siboga specimen should be as we describe from the conspecific Enewetak specimens.

Bergh was uncertain of the generic placement of his specimen, stating that he was unable to verify the arrangement of the gills (according to BERGH, 1891:129-130, tri- or quadripinnate gills are important to differentiate species of *Discodoris*). Although difficult to determine even in the living specimens from Enewetak, close examination found them to be tripinnate. However, the gill arrangement is not a differentiating characteristic, at the generic level, for this species.

Most characteristic and diagnostic for the generic placement of this species is the shape of the radular teeth. THOMPSON (1975:487) concisely describes the *Rostanga* radula: "radula broad, without median tooth, lateral teeth numerous and hook-shaped, marginal teeth bifid or multifid and brush-like." Comparison of our illustrations (Figures 2, 3) and BERGH's (1905:pl. XIV, figs. 23-28; reprinted here as Figure 6) with those of other species of

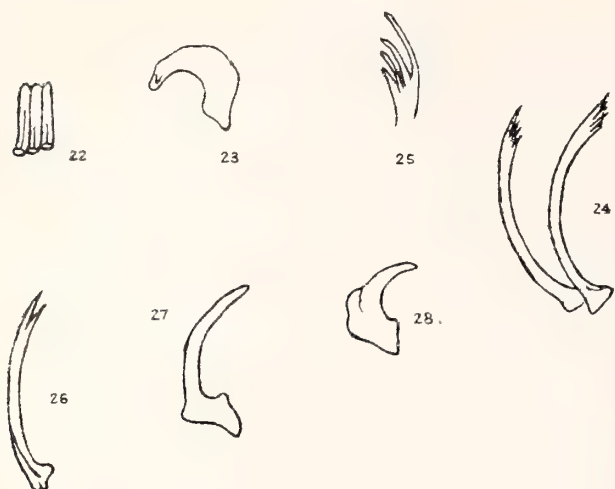


Figure 6

Reproduction of illustration of radular teeth by BERGH, 1905: pl. XIV, figs. 22-28.

Rostanga (e.g., MACFARLAND, 1966:pl. 35, figs. 1-8; THOMPSON, 1975:fig. 4; SCHMEKEL & PORTMANN, 1982: pl. 20, fig. 14; BABA, 1949:fig. 74) indubitably confirms our identification of this species as a *Rostanga*. Other features, such as reproductive system morphology and structure of the buccal elements, also match those of *Rostanga*. *Rostanga lutescens* is separable from the eight other species of *Rostanga* by its external coloration and radular characteristics (Table 1).

Rostanga hartleyi Burn, 1958, has simple hamate teeth; the innermost teeth have no accessory lateral denticle and the thin, outermost 5 or 6 marginal teeth do not have their tips split into a bifid or multifid arrangement (BURN, 1962: 164, fig. 15). The species probably should not be included in the genus *Rostanga*.

Externally, *Rostanga lutescens* bears considerable resemblance to *Jorunna alisonae* Marcus, 1976, and *Discodoris fragilis* (Alder & Hancock, 1864), both found in the same general area at Enewetak. *Jorunna alisonae* differs externally in its grayish color with darker grayish, variably sized circular spots, and internally in radular and reproductive system morphology (see the figures of *J. alisonae* in KAY & YOUNG, 1969:185, as *J. tomentosa*; and in MARCUS, 1976:40). *Discodoris fragilis* is much larger than *R. lutescens*, with more grayish coloration and more variation in the size of the dorsal, darker colored blotches (see the photographs in BERTSCH & JOHNSON, 1981:40).

Discodoris fragilis also lacks caryophyllidia, having simple tubercles. Again, radular tooth morphology easily separates the two species (see the figures in KAY & YOUNG, 1969:187; and in EDMUNDS, 1971:340).

This is apparently the first record of *Rostanga lutescens* since its original description from Timor, Indonesia (BERGH, 1905). The present collection from Enewetak (over 4500 km northeast of its type locality) indicates that the species is probably more widely distributed, at least in the western and west central Pacific.

ACKNOWLEDGMENTS

Many thanks to Lisa Boucher for diving assistance, including the collection of one of the specimens of *Rostanga lutescens*. Portions of this work were performed at the Mid-Pacific Research Laboratory, Enewetak, Marshall Islands.

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Patelloida chamorrorum spec. nov.: A New
Member of the Tethyan *Patelloida profunda*
Group (Gastropoda: Acmaeidae)

by

DAVID R. LINDBERG

Museum of Paleontology, University of California, Berkeley, California 94720

AND

GEERAT J. VERMEIJ

Department of Zoology, University of Maryland, College Park, Maryland 20742

Abstract. *Patelloida chamorrorum* spec. nov. from the Mariana Islands in the tropical western Pacific is described. The new species is a member of an ancient patellacean group that first appeared in the Eocene of the Paris Basin, and is today represented by scattered endemic populations throughout the tropics. This group, typified by *Patelloida profunda* Deshayes, is diagnosed for the first time and its distribution in space and time documented; members of the group are closely associated with calcareous substrates. *Patelloida deshayesia* nom. nov. is proposed as a replacement name for the homonym *Patella glabra* Deshayes.

INTRODUCTION

ONE OF THE MOST common gastropods of the rocky intertidal zone in Guam and other islands in the southern Marianas is an undescribed patellacean limpet of the genus *Patelloida*. Its recognition is significant not only because it contributes to a better understanding of the fauna of the Mariana Islands, but also because the new species is a member of an ancient lineage whose living members are scattered as endemic populations throughout the tropics. In this paper we describe the new species and outline its relationship to other living and fossil members of the *Patelloida profunda* group, a Tethyan clade that appears to be specialized for life on calcareous substrata.

Abbreviations are as follows: AHF—Allan Hancock Foundation (on permanent loan to LACM); ANSP—Malacology Department, Academy of Natural Sciences, Philadelphia, PA; CASIZ—Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, CA; LACM—Malacology Section, Natural History Museum of Los Angeles County, Los Angeles, CA; UCMP—Museum of Paleontology, University of California,

Berkeley, CA; USNM—Division of Mollusks, U.S. National Museum of Natural History, Washington, D.C.

SYSTEMATICS

ACMAEIDAE Forbes, 1850

PATELLOIDINAE Oliver, 1926

Shell: Shell composed of four layers. Outer surface of shell and interior margin complex prismatic. Next inner layer concentric crossed-lamellar, followed by myostracum, and radial crossed-lamellar layers.

Radula: Lateral teeth three pairs, uni- or multicuspid; marginal teeth two pairs or lacking. Ventral plates complex or simple.

Animal: Eyes present. Gut looping complex or highly simplified. Pericardial sac penetrated by rectum in some species. Excretory organs paired or with single right excretory organ and brood chamber. Gill typically present in nuchal cavity, but may be replaced by secondary gill in mantle groove, or absent.

Patelloida Quoy & Gaimard, 1834

Patelloida QUOY & GAIMARD, 1834:349, type-species by subsequent designation of GRAY, 1847:158, *Patelloida rugosa* Quoy & Gaimard, 1834.

Shell: Typically stout, with thick intermediate area composed of concentric crossed-lamellar layer. Sculpture variable but radial component usually present and concentric growth line sculpture typically threadlike and pronounced in complex prismatic layer.

Radula: Lateral teeth variable in size and shape; marginal teeth two pairs, cusps complex. Ventral plates complex; sutures, anterior processes and/or lateral extensions present in most taxa.

Animal: Gut looping complex; two excretory organs, one on either side of rectum; gill present in nuchal cavity. Oral lappets present in some species. Mantle edge often thickened with large tentacle/gland complexes.

Cretaceous to Recent. Past and present tropical and warm-temperate seas.

The *Patelloida profunda* Group

CHRISTIAENS (1975:93) first recognized the "*Patelloida profunda* Group," and referred several species to it, based on their resemblance (Table 1). The group is characterized for the first time as follows:

Light-colored shells of moderate to high profile. All slopes typically straight with rounded radial ribs; brown radial markings common. Ventral plates of radula complex with strong lateral processes and sutures; lateral teeth typically of equal size and shape. Recent species closely associated with calcareous substrates in tropical nearshore environments.

Patelloida chamorroorum

Lindberg & Vermeij, spec. nov.

(Figures 1–4, 10–12)

Patelloida flammea Quoy & Gaimard: HEDLEY, 1915:713 [non Quoy & Gaimard, 1834].

Patelloida sp.: VERMEIJ, 1971:316; VERMEIJ *et al.*, 1984 [in press].

Acmaea conoidalis auctt. [non Pease, 1868].

Shell (Figure 1): Shell of medium profile, apex slightly anterior of center. All slopes straight to weakly convex. Sculpture of approximately 35 primary ribs, smaller secondary ribs intercalated between most primary ribs. Radial sculpture overlain by rugose, concentric growth lines creating pustules on some primary ribs. Exterior of shell dirty white with 13 dark radial rays. Rays red-brown and intermittent on eroded portions of the shell. Interior margin white with dark markings corresponding to exterior rays. Intermediate area translucent white, with vague exterior rays. Central area strongly outlined by opaque white callus, tinted with orange-yellow.

Radula (Figures 2, 3): First pair of lateral teeth set

Table 1

Recent members of the *Patelloida profunda* group.

Taxon	Distribution
<i>Patelloida profunda</i>	Western Indian Ocean
<i>Patelloida profunda albonotata</i>	South Africa
<i>Patelloida profunda ivani</i>	Northwestern Australia
<i>Patelloida profunda mauritiana</i>	Mauritius
<i>Patelloida profunda omanensis</i>	Gulf of Oman
<i>Patelloida calamus</i>	Temperate Southern Australia
<i>Patelloida chamorroorum</i> *	Southern Marianas
<i>Patelloida conoidalis</i>	French Polynesia
<i>Patelloida pustulata</i> *	Caribbean
<i>Patelloida semirubida</i> *	Panamic
<i>Patelloida</i> sp.*	Java and New Guinea
<i>Patelloida</i> sp.*	Palau Group

* Newly assigned species.

close together on anterior edge of basal plates; cusps blunt. Second pair of lateral teeth directly posterior to first pair; cusps rounded. Third pair of lateral teeth lateral to second pair; cusps rounded. Lateral tooth edge elongated forming lateral extension that terminates near edge of ventral plates. Marginal teeth two pairs, cusps spoonlike; shafts elongate, terminating near middle of next posterior tooth row. First lateral plates tear-drop shaped, affixed to rounded anterior extension of the basal plate. Second lateral plates posterior to first plates; posterior edges straight, separated from third lateral plates by partial suture. Third lateral plates rounded. Ventral plates highly complex with anterior processes, lateral extensions, and strong anterior, posterior and lateral sutures. Posterior medial portion of plates marked with semicircular suture. Anterior edges of ventral plates concave, posterior edge convex.

Animal: Pigmentation lacking. Oral lappets present on snout, well-developed laterally and posteriorly; however, anterior portion of lappets weak (Figure 4). Mantle edge thickened with numerous large tentacle-gland complexes. These structures correspond to the fine crenulations around the perimeter of the aperture. Looping of the gut complex, intestine passing over digestive gland several times; eight sections of the intestine and stomach visible in some specimens (=4 loops).

Holotype dimensions: Length 14.1 mm, width 11.2 mm, height 5.9 mm.

Type locality: Mariana Islands: Guam; Asanite Bay (13°20'N, 144°46'E), leg. G. J. Vermeij, 10 July 1970.

Type material: Holotype UCMP 37522; 6 paratypes UCMP 37523. Paratypes have also been deposited in the collections of the USNM and LACM.

Distribution: Western Pacific: Mariana Islands; Cocos Island (AHF Acc. 1022)(13°14'N, 144°39'E), Guam [Type locality], Saipan (LACM 101634) (15°11'N, 145°45'E), and Tinian Island (LACM 101633)(14°58'N, 145°38'E).

Material examined: 18 lots, more than 100 specimens.

Etymology: The specific name, *chamorrorum*, is in honor of the Chamorro, the people of the Marianas.

Discussion: Other patellacean limpets in the Marianas that could be confused with *Patelloida chamorrorum* include small encrusted specimens of *Patella flexuosa* Quoy & Gaimard, 1834, and *Cellana radiata orientalis* (Pilsbry, 1891). *Patella flexuosa* has a lower profile and more irregular margin than *P. chamorrorum*. The central area of *P. flexuosa* is colored with orange-yellow; in *P. chamorrorum* the central area is only tinted. Radulae of the two species are quite different. *Patella flexuosa* has three pairs of marginal teeth, six pairs of lateral teeth, and a central tooth (3-6-1-6-3); *P. chamorrorum* has two pairs of marginal teeth, three pairs of lateral teeth, and lacks a central tooth (2-3-0-3-2). *Patella flexuosa* has a secondary gill; *P. chamorrorum* lacks a secondary gill.

Cellana radiata orientalis, which co-occurs with *Patella flexuosa* on wave-dashed algal ridges, differs from *Patelloida chamorrorum* in several important ways. The *Cellana* species has an irregular shell surface overlain by numerous, coarse riblets, and because of the uneven shell surface, the shell margin is also irregular. In *C. radiata orientalis* the shell structure is nacre-like (foliated) rather than porcelainous as in *P. chamorrorum*. The radular tooth formula of *C. radiata orientalis* is 3-2-0-2-3 and lacks a nuchal cavity gill but does have a secondary gill.

In their original description of *Patelloida flammea*, QUOY & GAIMARD (1834:354) reported this species from both Hobart-Town, Tasmania, and from Guam. HEDLEY (1915) proposed that *P. flammea* should be restricted to a species from Guam, and that the Tasmanian species was actually *Patella mixta* Reeve, 1855. However, IREDALE (1924) and OLIVER (1926) have pointed out that Quoy & Gaimard selected the Tasmanian species as the typical form of *P. flammea* (see PONDER & CREESE [1980] for a recent discussion of the identity of *P. flammea*). We agree that the species described and illustrated by Quoy & Gaimard as *P. flammea* is not from Guam, and more specifically, is not the species described herein as *P. chamorrorum*. QUOY & GAIMARD (1834) illustrated the snout of *P. flammea* (pl. 71, fig. 24). This drawing clearly shows weakly developed oral lappets (Figure 5); the oral lappets of *P. chamorrorum* are strongly developed (Figure 4), and the difference between these two states is too extreme to be a preservational artifact.

Specimens of the new species *Patelloida chamorrorum* have been confused with members of the *Patelloida profunda* (Deshayes, 1863) group. CHRISTIAENS (1975:93) referred *P. profunda* and the subspecies *P. p. albonotata* (Smith, 1901), *P. p. mauritiana* (Pilsbry, 1891), *P. p. omanensis* Christiaens, 1975, *P. p. ivani* Christiaens, 1975, plus *P. conoidalis* (Pease, 1868) and *P. calamus* (Crosse & Fischer, 1864), to this group stating that they had "a certain resemblance and probably the same ancestor." We

concur with Christiaens and refer *P. chamorrorum* to this group. *Patelloida chamorrorum* is distinguished from other members of the group by shell characters, external anatomy, and radular characters.

Patelloida chamorrorum has been often labeled in museum collections as *P. conoidalis* (Figure 6). Rib number and strength clearly define these two species. In *P. conoidalis* there are more ribs (50–60+) and the primary ribs are therefore narrower. The shell of *P. conoidalis* also has a stronger concentric sculpture that sometimes produces a cancellate pattern and the shell lacks coloration (no dark rays or red markings). Both species can have orange-yellow intermediate areas and the thickened central area can also be tinted. In the field the two species can be quickly distinguished by the shape of the oral lappets on the snout (cf. Figures 4, 7).

Patelloida chamorrorum differs from the nominal species of the group, *P. profunda*, by having fewer riblets, a more central apex, and by lacking the brown central area and white and light brown rays on the exterior shell surface. *Patelloida chamorrorum* differs from *P. calamus* (Figure 8) and *P. p. mauritiana* (Figure 9) in similar ways. Both *P. calamus* and *P. p. mauritiana* have more ribs (70–80+) than *P. chamorrorum* (30–40). In *P. calamus* the primary and secondary ribs are not well differentiated; both *P. chamorrorum* and *P. p. mauritiana* have distinct primary and secondary ribs. *Patelloida p. mauritiana* differs from *P. chamorrorum* by (1) having heavier, thread-like concentric growth lines that produce pustules at some intersections with the radial ribs, and (2) being dingy white in color and lacking radial rays and red markings. *Patelloida calamus* has fewer (6–8) dark rays than *P. chamorrorum*. In *P. calamus* the central area is sometimes red-pink; in *P. p. mauritiana* the intermediate area is often yellow-orange and thickened as in some specimens of *P. chamorrorum* (see Remarks below).

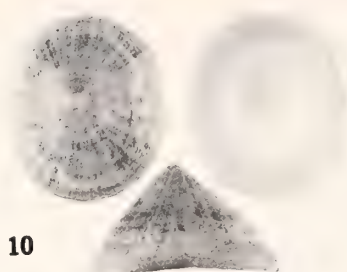
The radula of *Patelloida chamorrorum* clearly distinguishes it from other members of the *P. profunda* group. No previously recognized member of the *P. profunda* group has lateral extensions on the third lateral teeth (Figure 2).

Although the radulae are distinct in all members of this group, we are impressed by the similarities in both ventral plate and radular tooth morphologies. The differences between species in this group are more subtle than occur in other Patelloidinae (cf. PONDER & CREESE, 1980; LINDBERG, 1983) and in other genera (e.g., *Collisella*, *Lotia*, *Notoacmea*) (cf. MOSKALEV, 1970; PONDER & CREESE, 1980; LINDBERG & MCLEAN, 1981; LINDBERG, 1981).

Remarks: There is inter-island variation in shell characters. Specimens from Tinian are slightly larger (up to 25+ mm long) and have higher profiles than those from Guam and the more southern islands (Figure 10). These specimens have shells similar to those of *Patelloida conoidalis* and *P. p. mauritiana*. Specimens from the more southern Marianas tend to be lighter in color and have more



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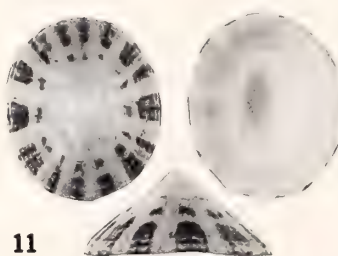
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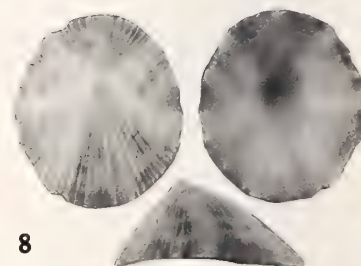
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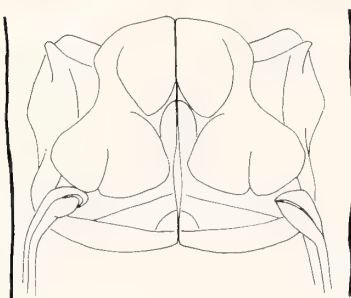
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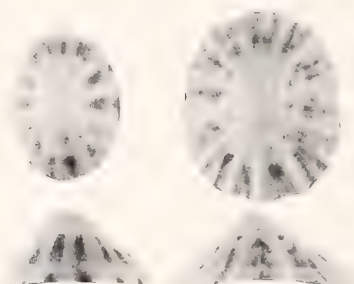
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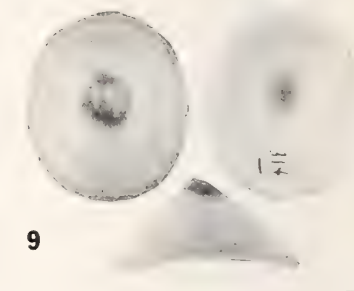
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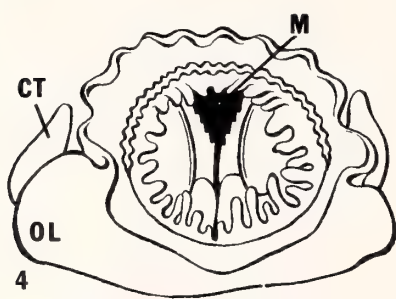
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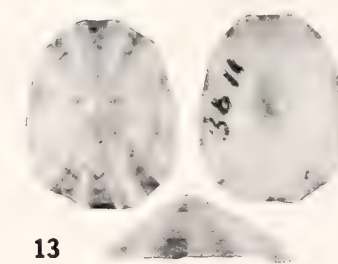
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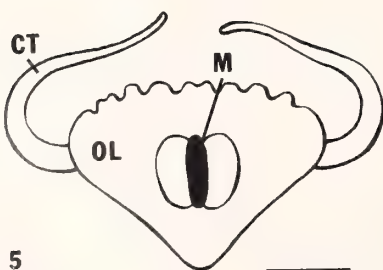
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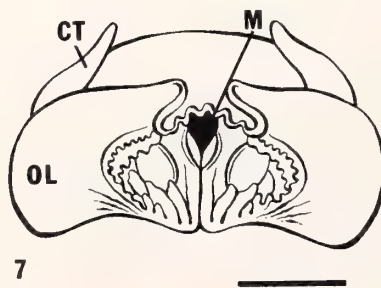
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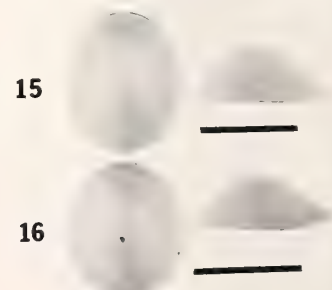
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vivid markings (Figure 11). While these markings are similar to those of *P. calamus* and other members of the *P. profunda* group (CHRISTIAENS, 1975), they most resemble the Recent New World *Patelloida*, *P. pustulata* (Helbling, 1777) and *P. semirubida* (Dall, 1914).

Juvenile shells of *Patelloida chamorrorum* have fewer ribs than the larger shells, and the radial color pattern is typically present (Figure 12). The intermittent red markings, which are found on some of the larger shells from Guam, are readily apparent on juvenile shells. These markings appear to be identical to the red markings found on some specimens of *P. pustulata* from the Caribbean (Figure 13).

Ecology and biogeography: *Patelloida chamorrorum* is an abundant limpet on the middle and upper shore of all the southern Mariana Islands, where it occupies pits (presumably of its own making) in the limestone. The chiton *Acanthopleura gemmata* (Sowerby, 1825) typically occurs with *P. chamorrorum*. We believe that *P. chamorrorum* is restricted to limestone shores. The species is not found on the volcanic shores of southwest Guam (VERMEIJ, 1971), and it is absent from the nine volcanic northern Mariana Islands (VERMEIJ *et al.*, 1984) (both as *Patelloida* sp.).

Patelloida chamorrorum is one of only a small handful of marine mollusks that are endemic to the southern Marianas. The only other confirmed example is the littorinid *Echininus viviparus* Rosewater, 1982, which, like *P. chamorrorum*, is an upper-shore species. *Echininus viviparus* is chiefly, but not exclusively, on limestone (VERMEIJ, 1971; ROSEWATER, 1982). Another possible endemic species is the small neritid *Nerita guamensis* Quoy & Gaimard, 1834. This species, or forms very much like it, is distributed in a disjunct fashion in the Philippines, Fiji, Samoa, the Ryukyus, the Izu Islands, and the northern and southern Marianas, and perhaps also the Natal coast of southeastern Africa. *Nerita guamensis* varies greatly from place to

place in the southern Marianas, especially in color, and lives with *E. viviparus* on the upper shore. It is striking that none of the upper-shore endemics of the southern Marianas are found in, or are closely related, to species inhabiting the atolls of the Marshall Islands, whose fauna is in most other respects similar to the Marianas. The disjunct distribution of the stocks to which the endemics belong suggests that the Mariana Islands may serve as a refuge for previously more widespread taxa in the tropical western Pacific.

DISCUSSION

The recognition of *Patelloida chamorrorum* in the Marianas and of its membership to the *Patelloida profunda* group caused us to examine closely the anatomical and shell characters of similar Recent members of the genus *Patelloida* and the shell characters of fossil species. From this work we have recognized additional Recent members of the *P. profunda* group in Indonesia, the tropical eastern Pacific, and Caribbean. Fossil members were identified from the Paleogene of Europe and the Neogene of the Caribbean.

In addition to the species listed by CHRISTIAENS (1975) and *Patelloida chamorrorum*, we would include *Patelloida* sp. (Java and New Guinea) (Figure 14), *Patelloida* sp. (Palau Group), *Patelloida semirubida* (Panamic), and *Patelloida pustulata* (Caribbean) in the *P. profunda* group (Table 1). Fossil members of this group are present in the Eocene rocks of the Paris Basin (*Patelloida centralis* [Deshayes, 1861] [Figure 15], *Patelloida deshajesia* nom. nov. [Figure 16]) and in materials recently collected in the Dominican Republic by Dr. Peter Jung and colleagues (*Patelloida* sp.) (Lindberg, unpublished data). Thus, Recent members of the *Patelloida profunda* group are distributed eastward from the east coast of Africa to the Caribbean. In the Eocene the group probably extended farther east to the Paris Basin of France, a clear and definite

Explanation of Figures 1 to 16

Scale bar = 10.0 mm except as noted.

Figures 1 to 4. *Patelloida chamorrorum* spec. nov. Figure 1. Holotype, UCMP 37522; Asanite Bay, Guam. Figures 2 and 3. Radular tooth and lateral plate morphology, LACM 77-16; Pago Bay, Guam. Scale bar = 0.1 mm. Figure 4. Ventral view of snout; oral lappets (ol), cephalic tentacles (ct), mouth (m) (museum data same as Figures 2 and 3). Scale bar = 1.0 mm.

Figure 5. Ventral view of snout of *Patelloida flammea*. Redrawn from QUOY & GAIMARD (1834; pl. 71, fig. 24). See Figure 4 for legend. Scale bar = 1.0 mm.

Figures 6 and 7. *Patelloida conoidalis*, LACM 69206; Henderson Island, Pitcairn Islands. Figure 6. Shell. Figure 7. Ventral view of snout. See Figure 4 for legend. Scale bar = 1.0 mm.

Figure 8. *Patelloida calamus*. Hypotype, UCMP 37524; Tumby Bay, Australia. Scale bar = 5.0 mm.

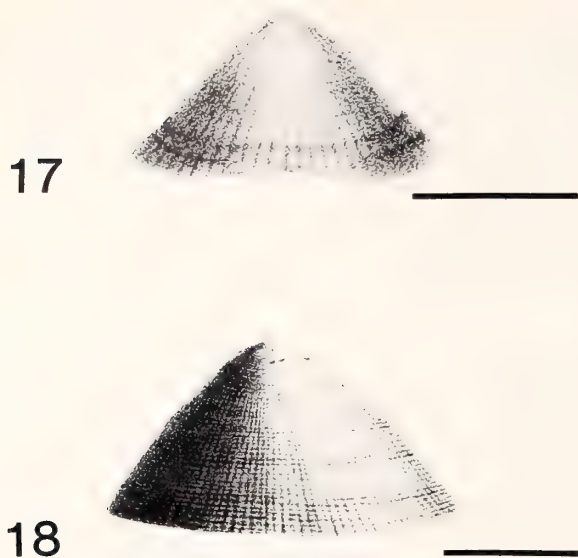
Figure 9. *Patelloida profunda mauritiana*. Hypotype, UCMP 37525; Mauritius.

Figures 10 to 12. *Patelloida chamorrorum* spec. nov. Figure 10. LACM 101628; Tinian Island. Figure 11. LACM 20342; Guam. Figure 12. LACM 77-3; Pago Bay, Guam. Scale bar = 5.0 mm.

Figure 13. *Patelloida pustulata*. LACM 35543; Bahama Islands.

Figure 14. *Patelloida* sp. Hypotype, UCMP 37526; Malinyping, Java.

Figures 15 and 16. Eocene *Patelloida* from the Paris Basin, France. Figure 15. *Patelloida centralis*. Hypotype, UCMP 37527. Scale bar = 5.0 mm. Figure 16. *Patelloida deshajesia* nom. nov. Hypotype, UCMP 37528. Scale bar = 5 mm.



Explanations for Figures 17 and 18

Scale bar = 10.0 mm.

Figure 17. Original illustration of *Patelloida conoidalis* from PEASE, 1868; pl. 11, fig. 22. Recent, Rarotonga Island, Cook Islands.

Figure 18. Original illustration of *Patelloida centralis* from DESHAYES, 1861; pl. 5, fig. 3. Eocene, Paris Basin, France.

Tethyan distribution in space and time (VERMEIJ, 1978: 227).

We characterize members of the *Patelloida profunda* group as having light-colored shells of moderate to high profile; rounded radial ribs and brown radial markings are typically present. The Recent species have complex radular ventral plates with strong lateral processes and sutures, and the lateral teeth are typically of equal size and shape. The Recent species are closely associated with calcareous substrates; members of this group are typically found on the abundant calcareous substrates and debris that predominate in tropical nearshore environments.

The fossil species were first identified using shell structure; all are members of the Patelloidinae and their shell morphology is identical to Recent members of the *Patelloida profunda* group. On some Eocene specimens from the Paris Basin, radial color patterns, similar to those of the Recent species, are still present. However, one of the most striking examples is seen by comparing the original illustration of the Recent *P. conoidalis* with the original illustration of the Eocene *P. centralis* (cf. Figures 17, 18). The differences that appear in these two illustrations are less than the intraspecific differences in most Recent species.

The similar shell morphology of members of the *Patelloida profunda* group has been responsible for many of the misidentifications of the species discussed herein, including *P. chamorroorum*. As stated above, *P. chamorroorum* has been most often misidentified as *P. conoidalis*. This is also true for other members of this group in the Indo-

Pacific. The *Patelloida* sp. from Java and New Guinea has been previously identified as *P. conoidalis* (CERNOHORSKY, 1972:38; pl. 6; fig. 5) and CHRISTIAENS (1980:77) has referred it to "*P. conoidalis* aff." from Hong Kong. At this time we have not seen an indisputable specimen of *P. conoidalis* from any locality farther west than the Cook Island group (160°W), and we suspect that, as in the case of *P. chamorroorum* in the Marianas, each *P. profunda* member in a major island group will prove to be distinct at the specific level. Currently, there is insufficient material, particularly whole animals, to describe the species from Java and New Guinea. However, shell characters do appear to distinguish this species from both *P. conoidalis* and *P. chamorroorum*. Another member of the *P. profunda* group for which there is insufficient material occurs on limestone cliffs at Urukthapel in the Palau Group (Vermeij, personal observation). The Palau Group species has more numerous radial ribs than *P. chamorroorum*.

The presence of a member of the *Patelloida profunda* group in the East Indies results in an almost continuous distribution for this group across the Pacific Ocean and into the Indian Ocean. However, we are suspicious of the apparent absence of a member of this group in the more northern islands of the East Indies (Celebes, Borneo, Philippines). A possible member in the Philippines may be "*Acmaea lentiginosa*" Reeve, 1855, reported by HIDALGO (1904) from Marinduque and Mindanao and by FAUSTINO (1928) from Marinduque and Surigao. We have not seen any specimens from the Philippines that are similar to Reeve's species and his description lacks locality data.

ACKNOWLEDGMENTS

We thank Welton L. Lee (CASIZ), James H. McLean (LACM), and Robert R. Robertson (ANSP) for providing loans of material from their respective institutions, and Mary E. Taylor (UCMP) for preparing Figures 4, 5, and 7. We are grateful to Joseph Christiaens (Hasselt, Belgium) for providing specimens to DRL for comparison and to Barry Roth (CAS) for furnishing Figure 17. We also thank Carole S. Hickman, James H. McLean, and an anonymous reviewer for commenting on the manuscript. This is contribution no. 207 from the University of Guam Marine Laboratory.

APPENDIX

Patelloida deshayesia nom. nov.

Figure 16

While preparing this paper, we found that primary homonymy exists between *Patella glabra* Turton, 1806, and *Patella glabra* Deshayes, 1824. *Patella glabra* TURTON, 1806:572 [vol. 4] is an unrecognizable, unlocalized brown limpet with white ribs. *Patella glabra* [DESHAYES, 1824: 10] is an Eocene *Patelloida* from Paris Basin localities in

France, and a junior primary homonym of *P. glabra* Turton, 1806. Therefore, we propose the name *Patelloida deshayesia* nom. nov. to replace *Patella glabra* Deshayes. The specific name is in honor of G. P. Deshayes who eloquently monographed the limpets (and other mollusks) of the Paris Basin.

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A New Species of *Cuthona* from the Gulf of California

by

DAVID W. BEHRENS

Pacific Gas and Electric Co., Biological Research Laboratory,
P.O. Box 117, Avila Beach, California 93424

Abstract. A new species, *Cuthona longi* Behrens, from the Gulf of California is described. This description represents the first occurrence of the genus *Cuthona* in the Gulf of California.

THE SYSTEMATIC status of *Catriona* Winckworth, 1941, *Cuthona* Alder & Hancock, 1855, and *Trinchesia* Ihering, 1879, has changed several times. The most recent revisions maintain *Cuthona* as a valid genus (GOSLINER & GRIF-FITHS, 1981) and recommend Tergipedidae Thiele, 1931, as the appropriate family designation (BROWN, 1980). BEHRENS (1984) reports 14 species of tergipedid nudibranchs for the northeastern Pacific, 12 of which are assigned to *Cuthona*. Collections made at Isla Raza, Baja California by Mr. Jeff Hamann included numerous specimens of a heretofore undescribed tergipedid nudibranch. To date there have been no cuthonid species reported from the Gulf of California, although at least two distinct species are known (J. R. Lance and T. M. Gosliner, personal communications; present study).

TERGIPEDIDAE Thiele, 1931

Cuthona Alder & Hancock, 1855

Cuthona longi Behrens, spec. nov.

(Figures 1 to 6)

Materials examined: (1) Holotype: one specimen approximately 10 mm long (preserved), collected in 3.1 m of water at Isla Raza, Baja California, Mexico (28°48'N, 113°0'W) in July 1982 by Jeff Hamann. This specimen is deposited in the collection of the California Academy of Sciences, Department of Invertebrate Zoology and Geology (CAS), CASIZ 053592.

(2) Paratypes: one specimen, 9 mm long (preserved), collected concurrently with the holotype is also deposited in the CAS collection, CASIZ 053593.

(3) One specimen, 10 mm long (preserved) collected concurrently with the holotype is deposited in the type collection of Los Angeles County Museum (LACM), Type Series No. 2085. Color transparencies of living *Cuthona longi* are on file at CAS and LACM.

Other material examined: (1) Six specimens, Isla Raza, Baja California; leg. D. W. Behrens, July 1982.

Description: Living animals measured up to 34 mm long. The body is typically aeolidiform, tapering posteriorly (Figures 1, 6). The foot is narrow, linear, tapering to a point posteriorly. The tail is short. The foot corners are rounded; only slightly laterally produced. The cephalic tentacles are cylindrical, tapering to a blunt tip and about $\frac{1}{2}$ the length of the rhinophores. The rhinophores are closely set, long, smooth, and tapering to a rounded tip. The cerata are cylindrical, linear with a conical tip, and attain a maximum length equal to about $\frac{2}{3}$ the length of the rhinophores (Figure 1). They are arranged in thirteen transverse rows dorsolaterally on the dorsum. The first row is situated immediately lateral to the rhinophores. The ceratal half formula from a series of large specimens is I 3-6, II 4-7, III 4-7, IV 5-8, V 6-7 (prepericardial); VI 5-6, VII 4-6, VIII 4-5, IX 4-5, X 3-4, XI 3, XII 2, XIII 1-2 (postpericardial). The ceratal arrangement is shown in Figure 2. The anal pore is anterior to the medial ceras of the sixth ceratal (first postpericardial) group and to the right of the pericardial elevation (Figure 2). The renal pore is just medial to the anal pore. The genital orifice lies below and between the first and second ceratal groups on the right side of the body (Figure 2).

The ground color of the body is pale yellow. Irregular patches of white and pale yellow pigment occur dorso-medially on the notum, head, and on the anterior surfaces of the rhinophores and cephalic tentacles. A pale blue rhomboidal patch occurs on the head, between the eyes and just posterior to the rhinophores. A smaller triangular patch of pale blue occurs anterior to and between the rhinophores. A few pale blue specks occur scattered over the notum. The distal $\frac{1}{3}$ of the rhinophores is encrusted with white pigmentation. The coloration of the cerata is complex (Figure 1b). The tip of each ceras is white, fol-

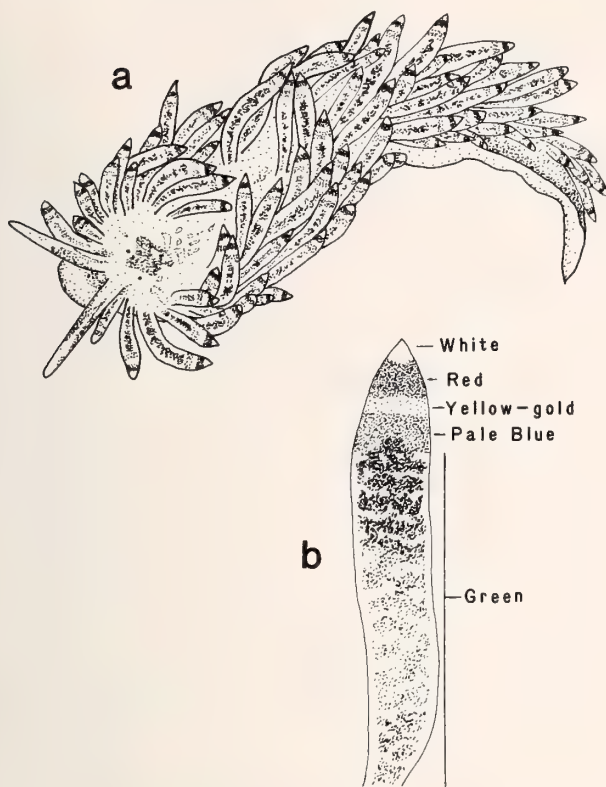


Figure 1

a. Dorsal view of *Cuthona longi* spec. nov., 10 mm in length. Isla Raza, Baja California. Drawn from color transparency. b. Ceras of *Cuthona longi* spec. nov. (Surface specks not shown.)

lowed by a subapical band of red. Below the red band is a thinner opaque yellow-gold band, followed by a slightly wider band of pale blue. Below this series of bands, the liver diverticulum appears granular in nature, fading in color from dark to light kelly green at the insertion. The entire surface of each ceras is speckled with opaque white specks.

The radular formula is $60-89 \times 0.1.0$. There are no preradular teeth. Each rachidian tooth is a low horseshoe-shaped arch, with a deep articulatory socket on the anterior surface on either side (Figure 3). The ceratal cusp forms a low ridge. There are 5 or 6 strong denticles to each side of the cusp, the largest being adjacent to the cusp and the others becoming smaller as they approach the side of the tooth. The jaws are lightly tinted gold and broadly oval (Figure 4a). The masticatory border is short with 30-45 irregular nodulous denticles (Figure 4b). In one of four specimens examined, a series of 3 or 4 hooks occurs below the non-hinged margin (Figure 4c). This feature, although probably an artifact, is mentioned because of its seemingly intentional presence on each plate of the jaw.

The reproductive system is typically cuthonid. The penial papilla is conical (Figure 5a). After dissection and

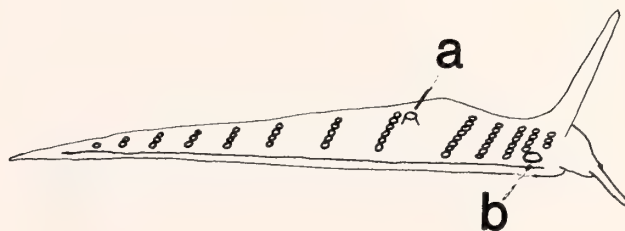


Figure 2

Diagrammatic right lateral view of the body of *Cuthona longi* spec. nov. a, anus; b, genital aperture.

clearing with 0.5 N quaternary ammonium hydroxide it was found to be unarmed. The ovotestis is massive containing large male acini with numerous smaller, peripheral female acini. The ampulla is convoluted. The vas deferens is short. The egg mass is a white semicircular coil attached to the substrate at the center of the whorl (Figure 5b). Its morphology does not fit HURST's (1967) classification. It is a combination of her Type A and Type D egg masses. The egg capsules are arranged within the ribbon in neat repetitive rows, radiating from the center of the crescent-shaped whorl. The region of attachment is thin and capsule-free. There were approximately 18-20 egg capsules per row and 50 rows per coil. The egg masses collected in July 1982 measured about 2.5 mm in diameter and were found on a leafy encrusting bryozoan growing at the base of a branched plumularid hydroid.

Discussion: Placement of *Cuthona longi* is based upon the presence of a non-tapering radula and the absence of a preradular tooth and penial stylet (GOSLINER & GRIF-

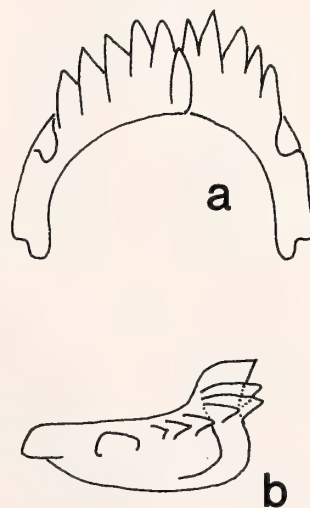


Figure 3

Radular teeth of *Cuthona longi* spec. nov. a, plain view; b, lateral view.

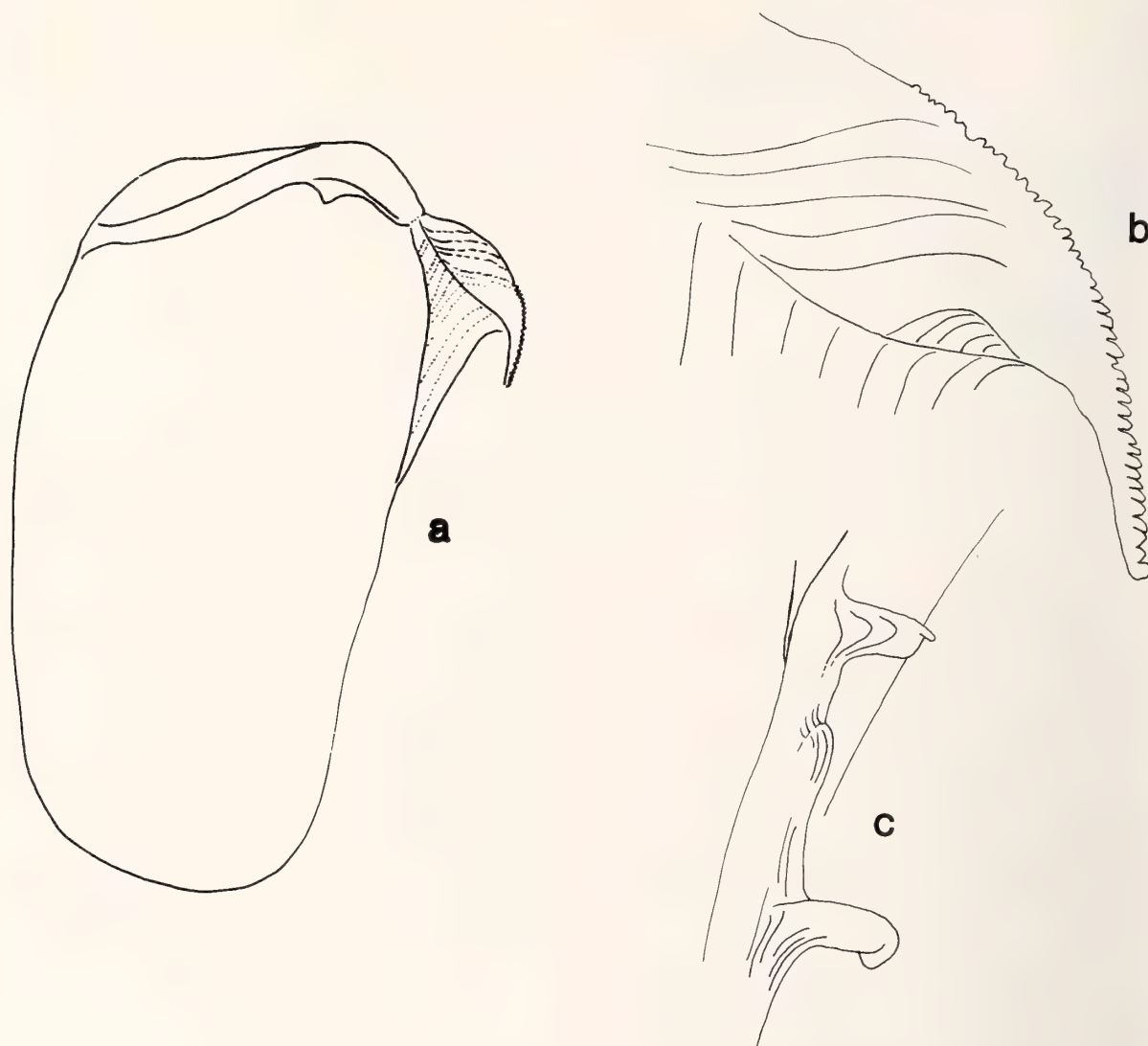


Figure 4

Jaw plate of *Cuthona longi* spec. nov. a, plain view; b, masticatory edge; c, hooks on margin of jaw.

FITHS, 1981). The species shares characteristics, however, with members of the genus *Catriona*, including a radula with greater than 50 teeth and the presence of bristles on the masticatory border of the jaw (GOSLINER & GRIFFITHS, 1981).

Cuthona longi is the first member of this genus to be described from the Gulf of California. Very few species assigned to this genus anywhere in the world exhibit blue pigmentation. *Cuthona caerulea* (Montagu, 1804) from the British Isles bears a brilliant blue ring medially on the cerata (THOMPSON & BROWN, 1976; BROWN & PICTON, 1979). In *C. speciosa* (Macnae, 1954) from South Africa the ceratal epithelium may be bright pale, luminescent blue (GOSLINER & GRIFFITHS, 1981). In *C. ornata* Baba, 1937, from Japan the ceratal core is cobalt blue (BABA,

1937). Only *C. genovae* (O'Donoghue, 1929) from the Mediterranean bears blue pigmentation on the body surface. In this species the head and prepericardial region is light blue with a medial white stripe (BOUCHET, 1976). The cerata also bear blue coloration.

Cuthona longi can be separated from northeastern Pacific species by its distinctive body and ceratal coloration and by its radula and jaw morphology. Pigmentation on the head region is not uncommon in *Cuthona*, as noted for *C. genovae* above; however, in the northeastern Pacific no species bears any pigmentation vaguely resembling that found on *C. longi*—a pale blue rhomboid patch on the head between the eyes and posterior to the rhinophores. In several species, *C. lagunae* (O'Donoghue, 1926), *C. perca* (Marcus, 1968), *C. abronia* (MacFarland, 1966), *C.*



Figure 5

a. Penis of *Cuthona longi* spec. nov. b. Egg mass of *Cuthona longi* spec. nov. (Not all eggs shown.)

albocrusta (MacFarland, 1966), *C. flavovulta* (MacFarland, 1966), and *C. virens* (MacFarland, 1966) ceratal core coloration may be green (BEHRENS, 1980, 1984; McDONALD, 1983); however, *C. longi* differs strikingly from all the above in the complex surface pigmentation of three distinct bands of color below a white apical tip, the opaque gold band being unique to the genus.

The length of the radula is similar to *Cuthona albocrusta*, *C. flavovulta*, and *C. lagunae*, having 60–89 teeth, all other species having shorter radulae (McDONALD, 1983). The masticatory border of the jaw has a much greater number of denticles (30–45) than other north-eastern Pacific species; however, the shape of the denticles is somewhat similar to those of *C. flavovulta*, *C. fulgens*, and *C. lagunae* (ROLLER, 1969; McDONALD, 1983).

The specific name *longi* is chosen to acknowledge the tireless efforts and scientific contributions of Mr. Steven J. Long, editor and publisher of *Shells and Sea Life*, previously the *Opisthobranch Newsletter*.

ACKNOWLEDGMENTS

I am grateful to Jeff Hamann for providing me with specimens and distributional data on this species, to Terry Gosliner for his assistance in differentiating this species



Figure 6

Cuthona longi spec. nov., 10 mm in length. Isla Raza, Baja California, Mexico. Photograph by Jeff Hamann.

from the dozens of cuthonid species worldwide, and to the referees for their careful review of the manuscript and constructive comments.

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Three New Species of *Lepidozона* (Mollusca: Polyplacophora) from the Gulf of California

by

ANTONIO J. FERREIRA¹

Research Associate, Department of Invertebrate Zoology, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118

Abstract. The number of species of *Lepidozона* endemic to the Gulf of California, Mexico, is raised to nine with the descriptions of three new ones, *L. laurae*, *L. macleaniana*, and *L. stohleri*, from the subtidal zone. A diagnostic key to the species of *Lepidozона* in the Gulf of California is given.

THE GENUS *Lepidozона* Pilsbry, 1892, is remarkably well represented in the northeastern Pacific. To the eight species already recognized in the temperate region (FERREIRA, 1978), and six others in tropical waters (FERREIRA, 1974), three new ones are added here to the fauna of the Gulf of California, raising to nine the number of *Lepidozона* species in the Panamic Province, and to seventeen the number in the northeastern Pacific.

Class Polyplacophora Gray, 1821

Order Neoloricata Bergenhayn, 1955

Suborder Ischnochitonina Bergenhayn, 1930

Family Ischnochitonidae Dall, 1889

Genus *Lepidozона* Pilsbry, 1892

Type-species: *Chiton mertensii* Middendorff, 1847, by original designation (PILSBRY, 1892).

Lepidozона laurae Ferreira, spec. nov.

(Figures 1 to 5)

Diagnosis: Small (largest, 14.5 mm long) chitons, rusty brown, carinate, not beaked. Anterior valve, lateral areas of intermediate valves, and postmucro area of posterior valve with very faint radial riblets, and minute, round tubercles (up to 80 μ m in diameter); central areas with longitudinal rows of granules coalescing into riblets, par-

allel to jugum, vaguely latticed; mucro anterior. Girdle with imbricate, striated scales. Radula with unicuspid major lateral teeth.

Type material: **Holotype** and one **paratype** at the California Academy of Sciences (CAS 050245 and CAS 050244, respectively); six other **paratypes** at the Los Angeles County Museum of Natural History (LACM 2003), United States National Museum of Natural History (USNM 820460), Academy of Natural Sciences of Philadelphia (ANSP 358901), and in the private collections of Laura and Carl Shy, Seal Beach, California, and Antonio J. Ferreira.

Type locality: 3.2 km southeast of San Antonio, Guaymas, Sonora, Mexico (27°57'N, 111°06'W), at 73-91 m (leg. Laura and Carl Shy, dredged Oct. 1977 and Oct. 1979).

Other material: 5 km south of Tetas de Cabra, Sonora, Mexico, dredged at 60-90 m, 2 specimens, largest 14 mm long (Skoglund Coll., leg. C. & P. Skoglund, Nov. 1979); 5 km southeast of Punta San Antonio, Guaymas, Sonora, Mexico, dredged at 100 m, 1 specimen, 14.5 mm long (Poorman Coll., leg. F. & L. Poorman, Apr. and Oct. 1983).

Description: **Holotype** (Figure 1), preserved flat in alcohol, 11.0 mm long, 6.5 mm wide (including girdle), 2.0 mm high; valves carinate, moderately elevated, posterior edge straight, not beaked; tegmentum microgranular. Lateral areas slightly elevated with 5-6 very faint radial riblets with minute (60-80 μ m in diameter), round tubercles

¹ For reprints: 2060 Clarmar Way, San Jose, California 95128.



Explanation of Figures 1 and 2

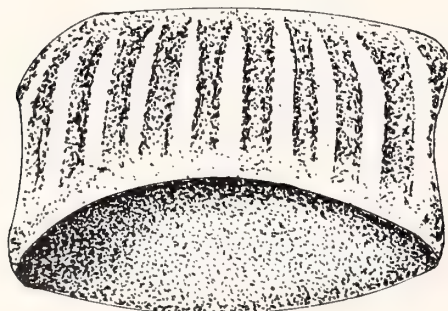
Figure 1. *Lepidozona laurae* Ferreira, spec. nov.: Holotype (CAS 050245).

Figure 2. *Lepidozona laurae* Ferreira, spec. nov.: Paratype, 13 mm long (Shy Coll.); close up of lateral areas of intermediate valves.

(see Figure 2, **paratype**); anterior valve with some 25 similar radial riblets and tubercles; central areas with longitudinal rows of granules, mostly coalesced into 12 riblets per side, vaguely latticed, and parallel to, but obsolete at jugum; on valve ii, few jugal riblets diverge in manner similar, although attenuated, to the wedgelike pattern seen in other species of *Lepidozona* (FERREIRA, 1974); mucro anterior; postmucro slightly concave with radial riblets and tubercles. Gills holobranchial, extending along 90% of foot's length, 20 plumes per side.

Paratype, 10.5 mm long, disarticulated: articulamentum white; slit formula, 10-1-11; insertion teeth sharp;

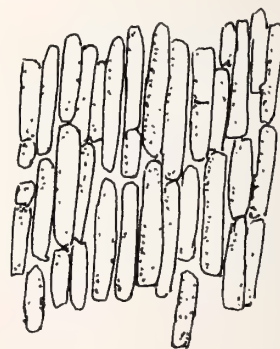
eaves solid; sutural plates subrectangular; sinus well defined; on valve viii, relative width of sinus (width of sinus/width of sutural plates), 0.4. Width of valve i/width of valve viii, 1.1. Girdle's upper surface covered with imbricate scales, up to 160 μm in length (smaller at inner and outer margins), with some 10 shallow striations (Figure 3); girdle's undersurface covered with elongate, transparent, rectangular scales, 40–80 μm long, 12 μm wide, arranged in columns as if articulated end-to-end (Figure 4). Radula (very similar to that of *L. mertensii* and other *Lepidozona* species [cf. fig. 34 in FERREIRA, 1978]), 3.5



100 μm

Figure 3

Lepidozona laurae Ferreira, spec. nov.: Paratype (Ferreira Coll.); scale of girdle's upper surface.



100 μm

Figure 4

Lepidozona laurae Ferreira, spec. nov.: Paratype (Ferreira Coll.); scales of girdle's undersurface.

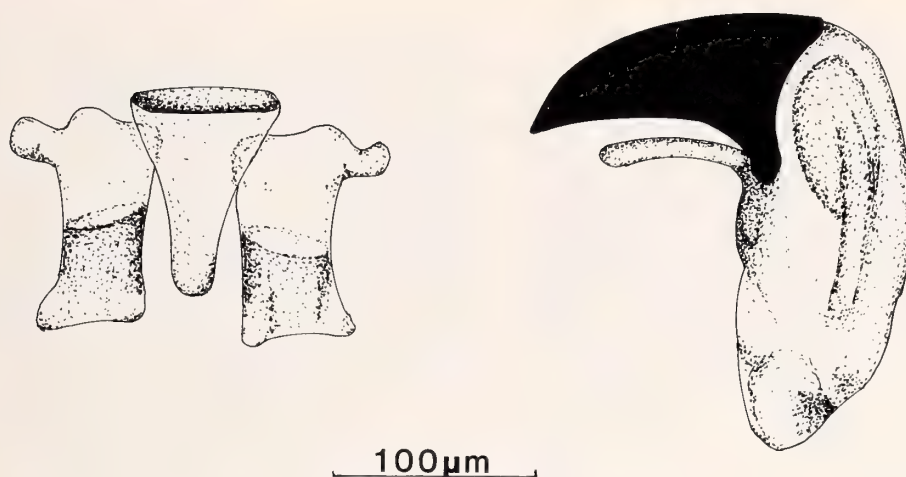


Figure 5

Lepidozona laurae Ferreira, spec. nov.: Paratype (Ferreira Coll.); radula's median, first lateral, and major lateral teeth.

mm long (33% of specimen's length), with 25 rows of mature teeth; median tooth enlarged at anterior blade, 80 μm wide, narrowing sharply posteriorly; first lateral teeth subrectangular, with explicit knob at antero-outer corner; major lateral teeth with unicuspid head, 70 μm wide, and unusually long and thin subcapital tubercle (Figure 5); outer marginal teeth elongate, 110 \times 70 μm .

Distribution: *Lepidozona laurae* is known only from the general locality of Guaymas, Sonora, Mexico, and depths of 60–100 m.

Remarks: For its striated scales, *Lepidozona laurae* may be grouped with the sympatric congeners *L. serrata* (Carpenter, 1864), *L. allynsmithi* Ferreira, 1974, *L. crockeri* (Willett, 1951), and *L. subtilis* Berry, 1956, from which it differs in sculptural features, size, color, and habitat (see FERREIRA, 1974). Because of its small size, and relatively deep-water habitat, rusty brown specimens of *L. laurae*, with small round tubercles on lateral areas and end valves, may be confused with *L. retiporosa* (Carpenter, 1864) known from similar latitudes in the outer (Pacific) colder side of Baja California; however, the two species differ distinctly in the tegmental sculpture of the central areas (granulose longitudinal riblets in *laurae*; quincuncial, netlike pits in *retiporosa*).

The species is here designated *laurae* after Laura Shy, Seal Beach, California, who, with her husband, Carl L. Shy, collected and kindly made available specimens for study.

Lepidozona macleani Ferreira, spec. nov.

(Figures 6 to 10)

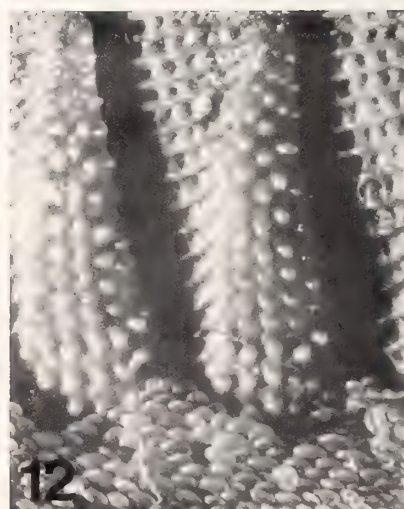
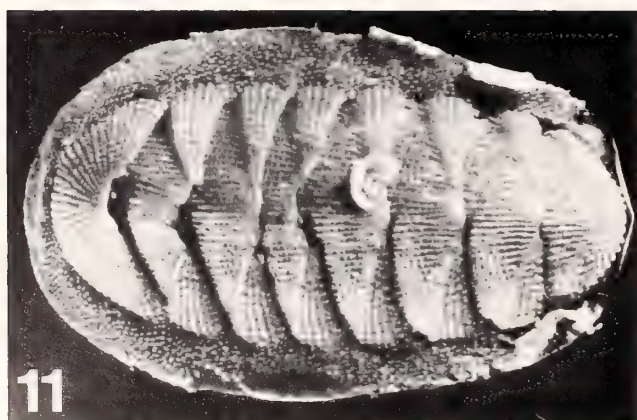
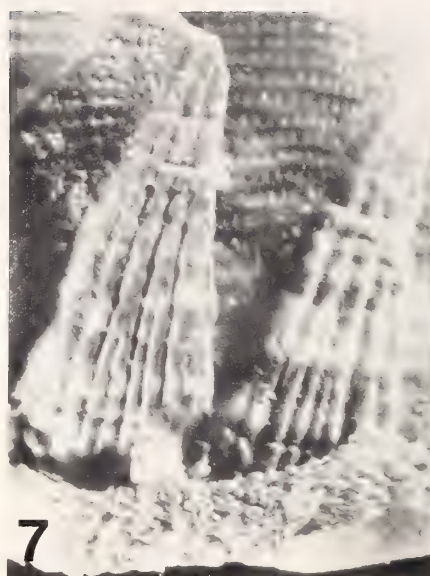
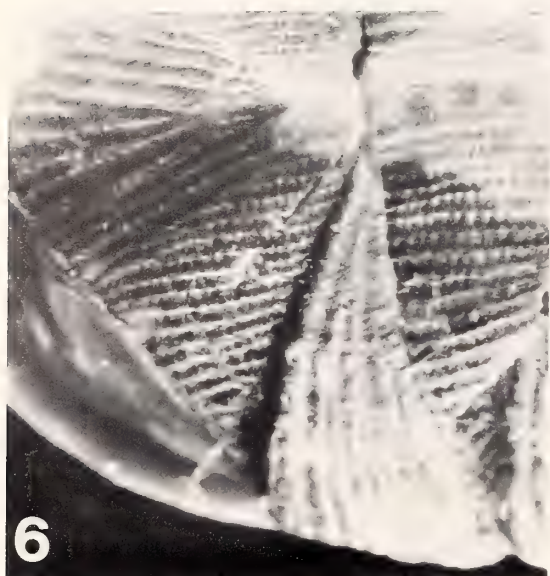
Diagnosis: Medium size (20 mm long) chiton, carinate, mottled cream-brown. Radial ribs flat, close together,

mostly smooth on lateral areas, irregularly granulose on end valves. Central areas with parallel, latticed, longitudinal riblets; jugum ribbed, with wedgelike pattern on valve ii. Mucro central. Girdle scales large, convex, smooth, nipped.

Type material: Holotype (LACM 2004).

Type locality: Off San Pedro Nolasco Island, Gulf of California, Mexico (27°58'32"N, 111°23'37"W), at 100–104 m (ex LACM-AHF 1085-40, 6 Feb. 1940).

Description: **Holotype** (Figures 6, 7, 8, 9), preserved in alcohol, valves iii–vii broken but in place; estimated length 20 mm long, width 10 mm, height 4 mm; valves carinate, not beaked; jugal angle about 110°; tegmentum microgranular, mottled cream-brown. Anterior valve with 30 radial flattish to subgranulose ribs, close together. Lateral areas with 6–8 radial ribs, similar to those on anterior valve, except for appearing much more decidedly flat, not granulose. Central areas with longitudinal riblets, parallel to jugum, 16 per side, about 70 μm thick, 150 μm apart, clearly latticed near jugum, but only obsoletely so in pleural areas; jugal areas ribbed, with wedgelike pattern on valve ii. Mucro central, postmucro area slightly concave with some 30 radial, flattish ribs. Articulamentum white with brown discoloration at apex of valves. Insertion teeth sharp, well formed; slits 12-1-12, followed by slit-rays; sutural laminae relatively short, subrectangular; sinus well defined; on valve viii, relative width of sinus, 0.3; width of valve i/width of valve viii, 1.1. Gills holobranchial, about 30 plumes per side. Girdle's upper surface covered with imbricate, strongly convex scales, up to 200 μm in length, some displaying nipplelike formation on dorsal edge (Figure 10); undersurface paved with transparent, rectangular scales, 60–80 μm long, 12 μm wide, arranged



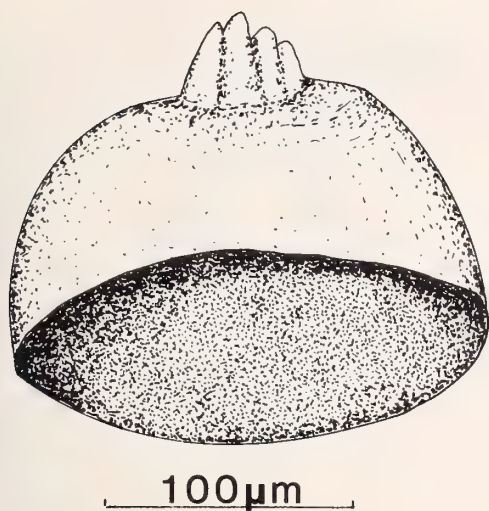


Figure 10

Lepidozona macleaniana Ferreira, spec. nov.: Holotype (LACM 2004); scale of girdle's upper surface.

end-to-end, in columns (as in *Lepidozona laurae*). Radula, not examined.

Distribution: *Lepidozona macleaniana* is known only from the type locality.

Remarks: For its strongly convex girdle scales, *Lepidozona macleaniana* resembles *L. formosa* from which it differs in tegmental sculpture (radial ribs of lateral areas flattish in *macleaniana*, distinctly tuberculate in *formosa*).

The species is here named *macleaniana* after Dr. James H. McLean, Los Angeles County Museum of Natural History, who has generously provided this and many other specimens for study.

Lepidozona stohleri Ferreira, spec. nov.

(Figures 11 to 14)

Diagnosis: Medium size (largest, 26 mm long) chitons, carinate, mostly brown-orange colored. Lateral areas and end valves with radial rows of small (to 200 μm), round tubercles. Central areas with longitudinal, parallel riblets, latticed: jugum ribbed, showing wedgelike pattern of rib-

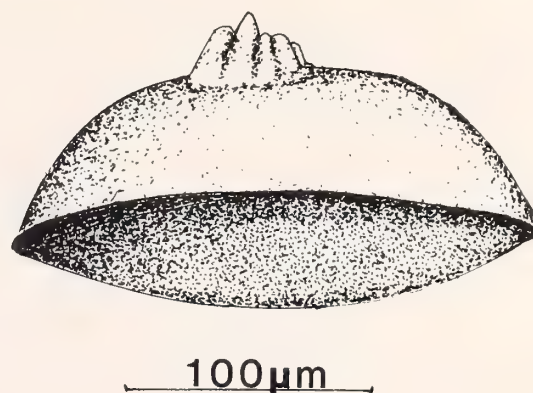


Figure 13

Lepidozona stohleri Ferreira, spec. nov.: Paratype (Ferreira Coll.); scale of girdle's upper surface.

lets on valve ii; mucro central. Girdle with large, smooth, convex, nipples scales.

Type material: Holotype (CAS 050246), and 16 paratypes (CAS 050247; LACM 2005; USNM 820459; ANSP 358902; and in the private collections of Laura and Carl Shy, and Antonio J. Ferreira).

Type locality: Smith Id., Bahía de Los Angeles, Gulf of California, Baja California, Mexico (29°02'N, 113°30'W), at 12–36 m (leg. Laura & Carl Shy, dredging, west side and south side of Smith Id., May 1975 and May 1976).

Other material: Puerto Refugio, Angel de la Guarda Id., Gulf of California, Mexico, 1 specimen, at 20–40 m (LACM-AHF 1048-40); Danzante Id., Gulf of California, Mexico, dredged at 30–60 m, 3 specimens, maximum 18 mm long (Shy Coll., leg. L. & P. Shy, Oct. 1982); Bahía de los Angeles, Baja California, Mexico, dredged at 21–50 m, 4 specimens, largest 18 mm long (Skoglund Coll., leg. C. & P. Skoglund, May 1976; Poorman Coll., leg. F. & L. Poorman, May 1976).

Description: Holotype (Figures 11, 12), preserved dry, flat, 20.5 mm long, 13 mm wide, uniformly orange. Valves carinate, not beaked, jugal angle 120°. Tegmentum microgranular. Anterior valve with 35 radial rows of round, discrete tubercles, about 100 μm in diameter (smaller to

Explanation of Figures 6 to 9, 11, and 12

Figure 6. *Lepidozona macleaniana* Ferreira, spec. nov.: Holotype (LACM 2004); close up of valves ii and iii.

Figure 7. *Lepidozona macleaniana* Ferreira, spec. nov.: Holotype (LACM 2004); close up of lateral areas of intermediate valves.

Figure 8. *Lepidozona macleaniana* Ferreira, spec. nov.: Holotype (LACM 2004); valves i and viii, tegmental surfaces.

Figure 9. *Lepidozona macleaniana* Ferreira, spec. nov.: Holotype (LACM 2004); valves i and viii, articular surfaces.

Figure 11. *Lepidozona stohleri* Ferreira, spec. nov.: Holotype (CAS 050246).

Figure 12. *Lepidozona stohleri* Ferreira, spec. nov.: Holotype (CAS 050246); close up of lateral areas of intermediate valves.

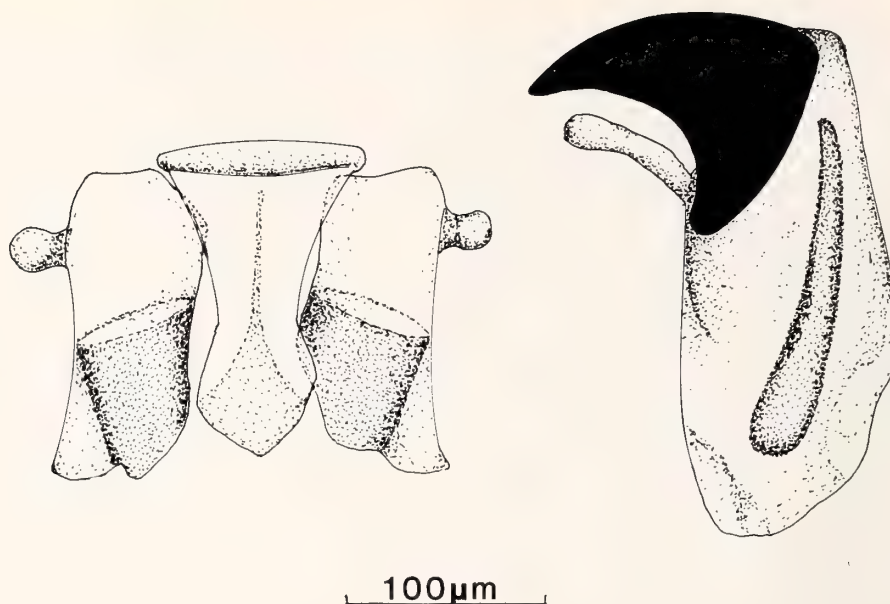


Figure 14

Lepidozona stohleri Ferreira, spec. nov.: Paratype (Ferreira Coll.); radula's median, first lateral and major lateral teeth.

50 μm centrally, larger to 200 μm at periphery), 100–150 μm apart. Lateral areas with 5–6 similar rows of tubercles; sutural edges irregularly crenulate by tubercles. Central areas with longitudinal riblets, 15–18 per side, parallel to jugum, 70 μm thick, 150 μm apart, latticed. Jugal areas, ribbed; riblets forming wedgelike pattern on valve ii. Mucro central; postmucral area somewhat convex, with some 20 similar radial rows of tubercles. Girdle's upper surface with imbricate, strongly convex scales, up to 200 μm in length, some showing nipplelike formation on dorsal edge (Figure 13); undersurface paved with transparent, rectangular scales, 60–80 μm in length, 10 μm in width, arranged end-to-end, in columns (as in *Lepidozona laurae*).

Paratypes uniformly brown-orange, except one with black pleural areas and white jugal stripe; none with red. Largest 26 mm long; width/length, mean = 0.63 ($n = 10$; $SD = 0.05$). Disarticulated paratype, 9.5 mm long; articulamentum, white; sutural laminae relatively short, subrectangular; insertion teeth well formed, sharp; slits 11–12, followed by slit-rays. On valve viii, relative width of sinus, 0.4; width of valve i/width of valve viii, 1.2. Gills holobranchial, about 20 plumes per side. Girdle, as in holotype. Radula, 4.2 mm long (44% of specimen's length), comprising 24 rows of mature teeth; median tooth 105 μm at anterior blade, narrowing posteriorly; first lateral teeth, subrectangular, 150 μm long, with large knob at antero-outer angle; major lateral teeth with unicuspid head, and subcapital tubercle long and thin (as in *Lepidozona laurae*, $37 \times 15 \mu\text{m}$ (Figure 14); outer marginal teeth, elongate, $150 \times 75 \mu\text{m}$.

Other material as above; one specimen from Danzante Id., and three specimens from Bahía de los Angeles with same black-white color pattern seen in one of the paratypes.

Distribution: *Lepidozona stohleri* is known only from Bahía de Los Angeles (type locality), Puerto Refugio, Angel de la Guarda Id. ($29^{\circ}32'33''\text{N}$, $113^{\circ}33'57''\text{W}$), and Danzante Id., Baja California, Mexico ($25^{\circ}46'\text{N}$, $111^{\circ}15'\text{W}$), at depths of 12–36 m to 30–60 m.

Remarks: *Lepidozona stohleri* may be confused with *L. formosa* Ferreira, 1974, from which it differs in the characteristics of the tubercles on lateral areas and end valves (coarsely defined, coalesced, like varices on the radial riblets in *formosa*; well defined, discrete, round, only occasionally coalesced in *stohleri*); in addition, the reddish hues often present in *L. formosa* have not been seen in *L. stohleri*.

On account of its large, convex, nipped girdle scales, *Lepidozona stohleri* belongs, with *L. macleani*, in the group of *L. clathrata* (Reeve, 1847) (see FERREIRA, 1974). Articulamentum and radula being identical, it is the presence of discrete tubercles on lateral areas and end valves that distinguishes it from these congeners in the Gulf of California. It also resembles the warm-temperate *L. mertensii* (Middendorff, 1847) and *L. guadalupensis* Ferreira, 1974; differential characteristics are found in the radial rows of tubercles on the anterior valve (about 35 rows, close together in *stohleri*; about 20 rows, well apart in *mertensii* and *guadalupensis*) and, similarly, on lateral areas.

The species is here named *stohleri* after Dr. Rudolf

Stohler, Research Zoologist Emeritus, University of California, Berkeley, California, founder and former Editor of *The Veliger*, to whom Californian malacologists will be forever indebted.

DISCUSSION

In addition to the three species here described, six other species of *Lepidozona*—*L. clathrata* (Reeve, 1847), *L. serrata* (Carpenter, 1864), *L. crockeri* (Willett, in Hertlein & Strong, 1951), *L. subtilis* Berry, 1956, *L. allynsmithi* Ferreira, 1974, and *L. formosa* Ferreira, 1974—are recognized in the Gulf of California, all endemic to the region. To facilitate their identification, the following key is given.

Key to the Species of *Lepidozona* in the Gulf of California

1. Girdle scales
 - large, convex, smooth, nipped 2
 - small, flattish, striated, not-nipped 5
2. Radial ribs in lateral areas and end valves
 - with tubercles 3
 - nearly smooth *L. macleaniana*
3. Tubercles
 - coalesced, like varices on rib 4
 - discrete, semispherical *L. stohleri*
4. Radial ribs (and color of specimens)
 - well apart, tubercles mostly elongate (specimens in dingy brown to greenish-gray tones) *L. clathrata*
 - close together, tubercles mostly round (specimens in bright, reddish tones) *L. formosa*
5. End valves and lateral areas
 - without tubercles 6
 - with tubercles 8
6. Radial ribs
 - of minute beads (5–8 riblets per lateral area) *L. subtilis*
 - flattened (2–4 per lateral area) 7
7. Central areas riblets
 - longitudinal, latticed *L. serrata*
 - crossed at oblique angles, forming lozenges *L. allynsmithi*
8. Tubercles
 - coalesced, like varices on rib *L. crockeri*
 - discrete, round *L. laurae*

ACKNOWLEDGMENTS

For their help and assistance, appreciation is here expressed to Laura and Carl L. Shy, Seal Beach, California; Carol and Paul E. Skoglund, Phoenix, Arizona; Forrest and Leroy Poorman, Westminster, California; Dr. James H. McLean, Los Angeles County Museum of Natural History; and Dr. Peter U. Rodda, California Academy of Sciences, San Francisco, California.

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Review of the West Coast Aspelloids *Aspella* and *Dermomurex* (Gastropoda: Muricidae), with the Descriptions of Two New Species

by

EMILY H. VOKES

Department of Geology, Tulane University, New Orleans, Louisiana 70118

Abstract. The ten known representatives of two closely related muricid genera, *Aspella* (four species) and *Dermomurex* (six species), living on the west coast of tropical America are discussed and figured. In *Aspella* these taxa include *A. pyramidalis*, *hastula*, and *pollux*. In *Dermomurex* the taxa are *D. obeliscus*, *indentatus*, *bakeri*, *cunninghamae*, and *myrakeenae*. In addition, two new species known only from Panamá are described: *Aspella strepta* and *Dermomurex gunteri*. Several Atlantic cognate species are also figured for comparison.

ONE WOULD THINK that the shallow-water molluscan fauna of tropical west America is among the best known in the world. But such is not the case; in the dozen years after KEEN published the second edition of *Sea Shells of Tropical West America* (1971) six new species of Muricidae alone were added (VOKES, 1983). The family Muricidae is a prominent part of the shallow-water fauna with almost 100 species. A relatively important member of this group is the genus *Dermomurex*, which until now had five known species; this paper adds a sixth. The genus *Aspella* has now four known species, with the addition of the new species described herein; no other geographic region except the western Atlantic has as many representatives of this small, and often overlooked, genus. Not only are there numerous species of *Aspella* and *Dermomurex* on the west coast of tropical America but there is an unusually large number of cognate species between the Atlantic and Pacific faunas.¹ Table 1 lists these parallel forms.

Both *Aspella* and *Dermomurex* normally occur in very shallow water, frequently under stones at low tide; only

the subgenus *Dermomurex* (*Trialatella*) occurs in offshore waters but the depth is still only about 60 m. This shallow-water habitat should mean that all forms had already been discovered; therefore, it was somewhat of a surprise recently to be given material from the Pacific coast of Panamá of what proved to be two new species of aspelloid.

The term "aspeloid" is an appellation, coined by me, to indicate the two genera *Aspella* and *Dermomurex*, which are united in having an extremely thick, deciduous, chalky outer layer. This peculiar layer, the *intritacalx* (D'ATTILIO & RADWIN, 1971), although not unique to the aspelloids, is not nearly as well developed in any other group, indicating that these two are more closely related to each other than to any other groups.

For many years *Dermomurex* was considered a subgenus of *Aspella* (e.g., KEEN, 1971:527) but work on their geologic history (VOKES, 1975) revealed a long separate development (back to the Oligocene) as well as several divisions that needed to be recognized within *Dermomurex*. The result is that *Aspella* is restricted to the nominate subgenus, with only 17 described species (fossil and Recent). *Dermomurex*, in contrast, is assigned five subgenera. The genus was discussed in a previous work (VOKES, 1975) and it was noted that there were 32 species, fossil and Recent, to be divided among these five subgenera. But, since that time, four additional Recent species have been added to the list: *D. alabastrum* (Adams) (see VOKES, 1976) and *D. oxum* Petuch (1979), both from the western At-

¹ In the family Muricidae, other than the aspelloids and excluding the subfamily Trophoninae, which is too poorly known to be discussed, in the tropical western Atlantic (Florida to northern Brazil) there are 99 species; in the tropical eastern Pacific (the area of Keen's study) there are 86 species. Of this number only 29 may be considered cognates (see VOKES, 1984, for more details).

lantic; *D. africanus* Vokes, 1978, from East Africa; and *D. bobyini* (Kosuge, 1984). The one described herein adds a fifth.

In addition to these Recent species I have in press two other papers in which a total of eleven species will be added: seven from Australia (two Recent and five fossil) and four fossils from the Dominican Republic. Thus, in less than ten years the number of taxa recognized has increased from 32 species to 48.

The same sort of development also can be seen in *Aspella* with the description of seven new species of *Aspella* by RADWIN & D'ATTILIO (1976:219–228) almost doubling the total count in one stroke. One additional species, *A. vokesiana*, from Madagascar, has since been described by HOUART (1983).

SYSTEMATIC DESCRIPTIONS

Family MURICIDAE Da Costa, 1776

Subfamily MURICINAE Da Costa, 1776

Genus *Aspella* Mörch, 1877

Aspella MÖRCH, 1877:24.

Type-species: *Ranella anceps* Lamarck, 1822, by monotypy.

Discussion: The genus *Aspella* is based upon a species of unknown provenance named by Lamarck as “*Ranella*” *anceps*. As members of the genus are so often, the original specimen is beach-worn, so that identification of the species is impossible. Originally it was confounded with the west coast *A. pyramidalis* (Broderip), but the latter is one of the few *Aspella* species that cannot be confused with *A. anceps*, due to its color pattern.

I formerly (VOKES, 1975, 1978) considered *Aspella anceps* to be the species later described as *A. acuticostata* (Turton, 1932), from South Africa, which I thought also occurred in Australia (the latter subsequently described as *A. ponderi* by RADWIN & D'ATTILIO, 1976).

Since that time Winston Ponder, of the Australian Museum, has located Lamarck's type specimen, which is in the Geneva Museum and, although it did not solve the problem, it did eliminate some of the contenders. Assuming it is one of the described species, we may compare it with the following: *Aspella acuticostata* (Turton, 1932), from South Africa; and *A. ponderi* (Australia), *mauritana* (Mauritius), *cryptica* (Brazil), and *platylaevis* (Indo-Pacific, in general), all of Radwin & D'Attilio, 1976. Of these, *acuticostata*, *mauritana*, and *cryptica* are all too small, as the type is about 14 mm in height. The Australian *A. ponderi* is a possibility at just under 14 mm, but the most likely candidate seems to be *A. platylaevis*. It is the largest species with the proper shape (*i.e.*, a narrow shell unlike the more alate, larger species, such as *A. producta*) and it has the most widespread distribution, being known from Western Australia and Palau, to the Philippine Islands

Table 1
Atlantic-Pacific cognate species of aspelloids.

Pacific form	Atlantic form
<i>Aspella</i>	
<i>A. pyramidalis</i> (Broderip)	<i>A. cryptica</i> Radwin & D'Attilio
<i>A. hastula</i> (Reeve)	<i>A. morchi</i> Radwin & D'Attilio
<i>A. pollux</i> Radwin & D'Attilio	<i>A. castor</i> Radwin & D'Attilio
—	<i>A. senex</i> Dall
<i>A. strepta</i> , spec. nov.	—
<i>Dermomurex</i>	
<i>D. obeliscus</i> (A. Adams)	<i>D. pauperculus</i> (C. B. Adams)
<i>D. indentatus</i> (Carpenter)	<i>D. alabastrum</i> (A. Adams)
<i>D. gunteri</i> , spec. nov.	—
<i>D. bakeri</i> (Hertlein & Strong)	<i>D. elizabethae</i> (McGinty)
<i>D. cunningghamiae</i> (Berry)	<i>D. abyssicola</i> (Crosse)
—	<i>D. oxum</i> Petuch
<i>D. myrakeenae</i> (Emerson & D'Attilio)	—

and French Polynesia (Rangiroa and Tahiti—Vokes Coll.). Thus, *A. platylaevis* seems the most likely candidate for identification as Lamarck's species. However, as RADWIN & D'ATTILIO state (1976:21), whatever species might ultimately be proven to be the “real” *A. anceps*, nothing would be changed in the generic concept of *Aspella*, so similar are all the forms.

Aspella pyramidalis (Broderip, 1833)
(Figures 1–3)

- Ranella pyramidalis* BRODERIP, 1833:194: SOWERBY, 1835: pl. 84, fig. 2.
Ranella anceps Lamarck: KIENER, 1842:37 (locality data only) not pl. 4, fig. 2 (? = type specimen of *anceps*); REEVE, 1844a:pl. 8, fig. 43 (not of Lamarck).
Aspella (*Aspella*) *pyramidalis* (Broderip): KEEN, 1958b:364, not fig. 376 (= *A. pollux* Radwin & D'Attilio); KEEN, 1971:527, fig. 1013 (syntypes, British Museum).
Aspella pyramidalis (Broderip): VOKES, 1975:125, pl. 1, figs. 10–13; RADWIN & D'ATTILIO, 1976:23, pl. 1, figs. 4–6 only; text figs. 7 (intritacalx), 8 (radula); FAIR, 1976: 70, pl. 16, figs. 205–207.

Discussion: *Aspella pyramidalis* is by far the most common species of *Aspella* on the tropical west coast, ranging from Mazatlán, Mexico, to Panamá (Vokes Coll.), and as far south as Colombia (*vide* RADWIN & D'ATTILIO, 1976:25). This distribution is undoubtedly a reflection of the longer larval stage indicated by the three and three-quarter whorl protoconch, which in *Aspella* is unique to *A. pyramidalis*. All other species have paucispiral protoconchs. It has been cited from the Galápagos, but (so far as I know) all specimens taken there are to be referred to *A. hastula*, which follows.

Aspella hastula (Reeve, 1844)

(Figure 4)

Ranella hastula REEVE, 1844a:pl. 8, fig. 42; REEVE, 1844b: 139.

Aspella pyramidalis (Broderip): HERTLEIN & STRONG, 1939: 369, pl. 32, figs. 10, 13 (not of Broderip).

Aspella (*Aspella*) *hastula* (Reeve): KEEN, 1971:527, fig. 1012.

Aspella hastula (Reeve): VOKES, 1975:126, pl. 1, fig. 8; FAIR, 1976:47, pl. 16, fig. 208.

Aspella pyramidalis (Broderip): RADWIN & D'ATTILIO, 1976: 24, in part, pl. 1, figs. 7, 8 only.

Discussion: This species is sometimes included with *Aspella pyramidalis*; however, it may be distinguished by the spiral rows of nodes or granulations that mark the shell. RADWIN & D'ATTILIO (1976:24) believed that Reeve's illustration was of the mainland form (*A. pyramidalis*). This seems unlikely for two reasons: one, Reeve specifically mentioned that the shell is "transversely granulately striated," and, two, he compared it with "*Ranella anceps*" (which to him was *A. pyramidalis*) stating that it is "less pyramidal" although similar to that species. It seems obvious that he was distinguishing between the two west American species.

Although Reeve gave no locality for the species he named "*R.*" *hastula*, it is almost certainly the Galápagos snail, as this is the only living species known that has granulations (there is one [?]unnamed European Miocene form that is granulated). Granules are also shown in the specimen illustrated by HERTLEIN & STRONG (1939:pl. 32, fig. 10)

said to come from the Pleistocene raised beach on San Salvador Island (James), Galápagos.

Aspella pollux Radwin & D'Attilio, 1976

(Figure 5)

Aspella (*Aspella*) *pyramidalis* (Broderip): KEEN, 1958b:364, in part, fig. 376 only.

Aspella cf. *A. pyramidalis* (Broderip): D'ATTILIO & RADWIN, 1971:356, fig. 4 (intritacalx).

Aspella sp.: VOKES, 1975:126, pl. 1, fig. 9; FAIR, 1976: 88, pl. 16, fig. 211.

Aspella pollux RADWIN & D'ATTILIO, 1976:225, pl. 1, figs. 3, 29, text-figs. 172 (intritacalx), 173 (radula).

Discussion: This species, which has only recently been recognized as distinct from the more abundant *Aspella pyramidalis*, is the eastern Pacific equivalent of *A. producta* in the Indo-Pacific, with a much larger and wider shell form. RADWIN & D'ATTILIO (1976:226) note that it is found from the Gulf of California to Costa Rica, but as yet it has not been taken in Panamá or farther south.

Aspella strepta E. H. Vokes, spec. nov.

(Figures 6, 7)

Description: Shell small, six teleoconch whorls, protoconch unknown. On first postnuclear whorl six rounded axial ridges; by third postnuclear whorl two of these strengthened into small varices on opposite sides of the shell, with a second set of weaker ribs formed from the

Explanation of Figures 1 to 14

Figures 1, 2, 3. *Aspella pyramidalis* (Broderip). Locality of all: TU R-166, Barra de Navidad, Jalisco, Mexico.

Figure 1. (×3). USNM 739569; height 13.5 mm, diameter 5.7 mm. With intritacalx present.

Figure 2. (×3). USNM 739569; height 12.7 mm, diameter 5.5 mm. With intritacalx removed, showing underlying color pattern.

Figure 3. (×3). USNM 739569; height 15.0 mm, diameter 6.5 mm.

Figure 4. *Aspella hastula* (Reeve). (×3). USNM 739567; height 12.4 mm, diameter 6.0 mm. Locality: Galápagos Islands, Ecuador.

Figure 5. *Aspella pollux* Radwin & D'Attilio. (×3). USNM 739568; height 13.5 mm, diameter 7.0 mm. Locality: TU R-166, Barra de Navidad, Jalisco, Mexico.

Figures 6, 7. *Aspella strepta* E. H. Vokes, spec. nov. Locality of both: Azuero Peninsula, Panamá.

Figure 6. (×4). USNM 838031 (holotype); height 11.5 mm, diameter 3.3 mm.

Figure 7. (×4). USNM 838032 (paratype); height 11.2 mm, diameter 5.0 mm. With intritacalx removed, showing underlying color pattern.

Figures 8, 9. *Dermomurex* (*Gracilmurex*) *bakeri* (Hertlein & Strong). Locality of both: Manzanillo, Colima, Mexico.

Figure 8. (×3). Purdy Coll.; height 17.5 mm, diameter 8.5 mm.

Figure 9. (×4). Purdy Coll.; height 13.4 mm, diameter 5.5 mm. With intritacalx removed, showing underlying color pattern.

Figure 10. *Dermomurex* (*Gracilmurex*) *elizabethae* (McGinty). (×4). ANSP 176449 (holotype); height 12.5 mm, diameter 5.8 mm. Locality: Middle Sambo Shoals, Florida.

Figure 11. *Dermomurex* (*Trialatella*) *cunninghamae* (Berry). (×3). SUPTC 9502 (holotype); height 18.0 mm, diameter 9.2 mm. Locality: Puerto San Carlos, Sonora, Mexico.

Figures 12, 13. *Dermomurex* (*Trialatella*) *oxum* Petuch.

Figure 12. (×3). USNM 780648 (holotype); height 12.5 mm, diameter 6.6 mm. Locality: Abrolhos Archipelago, Bahia, Brazil.

Figure 13. (×3). USNM 739571; height 9.0 mm, diameter 4.0 mm. Locality: TU R-98, Holandes Cay, off Cape San Blas, Panamá.

Figure 14. *Dermomurex* (*Trialatella*) *abyssicola* (Crosse). (×3). MHNP; height 10.1 mm, diameter 5.6 mm. Locality: Guadeloupe, French Antilles.

Note: Except as indicated, all specimens whitened to show details of ornamentation.



pair of ridges immediately abapertural to these, the third pair being reduced to buttresses across the suture. On fifth postnuclear whorl an abrupt change of alignment, with 240° between one varix and the next formed; varical formation thereafter only every 240°, creating a 60° offset from each varix to the corresponding one on the previous whorl, instead of being aligned up the spire as in the earlier whorls; presence of former varical positions indicated by buttresses across the suture. Except for the varices, shell surface almost totally smooth and polished. Aperture elongate-oval, inner lip appressed, unornamented; inner side of outer lip with six small elongate denticles. Siphonal canal short, dorsally recurved at distal end. Shell covered with a thick intritacalx, marked only by a very faint axial striae; when worn revealing a color pattern consisting of a single brown band covering the area from periphery to suture; apertural denticles tipped with brown.

Holotype: USNM 838031.

Dimensions of holotype: Height 11.5 mm, diameter 3.3 mm.

Type locality: Azuero Peninsula, Panama (approximately 7°15'N, 8°30'W), John Gunter Coll.

Paratype: USNM 838032; height 11.2 mm, diameter 5.0 mm; locality same as holotype.

Discussion: This new species seems very closely related to *Aspella pyramidalis*, which also occurs in Panamá. The obvious difference is the peculiar offset in the later whorls, giving rise to the twisted appearance of the shell indicated by the species name (Greek—*streptos*, twisted). The color pattern, the nature of the intritacalx, and the form of the aperture are all extremely close to *A. pyramidalis*. It is unfortunate that none of the specimens in the type lot have the protoconch preserved, for this might be a definitive difference. At the present time, it is not inconceivable that these specimens represent an atypical population of *A. pyramidalis* but this seems unlikely.

The only other differences noted are that the spire of

Aspella strepta is higher and narrower than *A. pyramidalis*, even in the early stages before the twisting occurs, and the pronounced dorsoventral flattening is not as evident in the new species. Also, the spiral lines seen in the intritacalx of *A. pyramidalis* do not seem to be present in *A. strepta*.

The type lot consists of only three specimens, all collected under stones at low tide by Mr. John Gunter, Panamá City, Panamá, and generously given to me for study. No other specimens are known.

Genus *Dermomurex* Monterosato, 1890

Poweria MONTEROSATO, 1884:113. (Non *Poweria* Bonaparte, 1840.)

Type-species: *Murex scalarinus* Bivona-Bernardi, by original designation (*Murex scalarinus* Bivona-Bernardi, 1832, = *Murex scalaroides* Blainville, 1829).

Dermomurex MONTEROSATO, 1890:181. New name for *Poweria* Monterosato non Bonaparte.

Hexachorda COSSMANN, 1903:47.

Type-species: *Murex tenellus* Mayer, 1869, by original designation.

Subgenus *Dermomurex* s.s.

Dermomurex (Dermomurex) obeliscus
(A. Adams, 1853)

(Figure 18)

Murex obeliscus A. ADAMS, 1853:269; SOWERBY, 1879:fig. 233.

Aspella (?*Dermomurex*) *obeliscus* (Adams): EMERSON & D'ATTILIO, 1970:91, figs. 7–9 (figs. 8, 9, syntypes, British Museum); KEEN, 1971:527, fig. 1016.

Dermomurex obeliscus (Adams): D'ATTILIO & RADWIN, 1971:346, figs. 1, 6 (intritacalx); RADWIN & D'ATTILIO, 1976:46, pl. 1, figs. 21–24, text-fig. 23 (radula); FAIR, 1976:63, pl. 16, fig. 222.

Dermomurex (Dermomurex) obeliscus (Adams): VOKES, 1975:127.

Discussion: First described without locality data, then ascribed to the Caribbean by SOWERBY (1879:pl. 23, fig.

Explanation of Figures 15 to 21

Figures 15, 16. *Dermomurex (Dermomurex) gunteri* E. H. Vokes, spec. nov. Locality of both: Los Buzos, Combutal, Azuero Peninsula, Panamá.

Figure 15. (×3). USNM 838035 (holotype); height 20.0 mm, diameter 8.4 mm.

Figure 16. (×3). USNM 838036 (paratype); height 15.3 mm, diameter 7.0 mm.

Figure 17. *Dermomurex (Takia) myraekeanae* (Emerson & D'Attilio). (×3). Wright Coll. M-309; height 16.3 mm, diameter 9.0 mm. Locality: West Mexico.

Figure 18. *Dermomurex (Dermomurex) obeliscus* (A. Adams).

(×2½). USNM 838038; height 23.5 mm, diameter 11.0 mm. Locality: Isla Islote, Nayarit, Mexico.

Figure 19. *Dermomurex (Dermomurex) pauperculus* (C. B. Adams). (×2). MCZ 125072; height 30.0 mm, diameter 14.8 mm. Locality: Causeway, Biscayne Bay, Miami, Florida.

Figure 20. *Dermomurex (Dermomurex) indentatus* (Carpenter). (×2). Gunter Coll.; height 29.0 mm, diameter 13.6 mm. Locality: Montijo Bay, Panamá.

Figure 21. *Dermomurex (Dermomurex) alabastrum* (A. Adams). (×2). AMNH 186115; height 29.0 mm, diameter 13.0 mm. Locality: St. Croix, Virgin Islands.

Note: All specimens whitened to show details of ornamentation.



233), it was not until 1970 that EMERSON & D'ATTILIO (1970:91) demonstrated that this species is a member of the west American fauna. The shell usually cited as "*Murex obeliscus*" from the Caribbean is *Dermomurex pauperculus* (C. B. Adams), which is indeed the Atlantic cognate of *D. obeliscus* (see Figure 19), but it is not the same species.

This is the most common of the west coast species of *Dermomurex*, being found under stones at low tide, from Mazatlán to Panamá.

Dermomurex (Dermomurex) indentatus
(Carpenter, 1857)

(Figure 20)

Muricidea (?) erinaceoides var. *indentatus* CARPENTER, 1857: 527.

Aspella (Dermomurex) perplexa KEEN, 1958a:248, pl. 30, fig. 11 (only).

Aspella (?) Dermomurex) indentatus (Carpenter): KEEN, 1958b: 365, fig. 378 (with *A. perplexa* in synonymy).

Muricidea (?) erinaceoides var. *indentatus* Carpenter: KEEN, 1968:425, pl. 58, fig. 64 (holotype, British Museum).

Aspella (?) Dermomurex) indentatus (Carpenter): EMERSON & D'ATTILIO, 1970:90, fig. 3.

Aspella (Dermomurex) indentatus (Carpenter): KEEN, 1971: 527, fig. 1014 (left fig. = holotype *A. perplexa* Keen; right fig. = holotype "*M.*" *indentatus*).

Dermomurex (Dermomurex) indentatus (Carpenter): VOKES, 1975:127.

Dermomurex indentatus (Carpenter): RADWIN & D'ATTILIO, 1976:46, pl. 1, fig. 17; FAIR, 1976:50, pl. 16, fig. 218.

Discussion: Although described in 1857, this species was not illustrated for one hundred years (KEEN, 1958b:fig. 378), and it was not until 1968 that a figure of the holotype was published (KEEN, 1968:pl. 58, fig. 64). In 1970 EMERSON & D'ATTILIO discussed "*Aspella*" *indentatus* and noted that it was "rare in collections." This situation has not changed; to my knowledge it is known only from Pacific Panamá and Sonora, Mexico, near the type locality, Mazatlán (AMNH 180694).

The western Atlantic cognate of this species is the equally poorly known *Dermomurex alabastrum* (A. Adams) (see Figure 21), which I once suggested was probably a synonym of *D. indentatus* (VOKES, 1975:140), as I had never seen a specimen of the Atlantic species. This error was corrected in a note on *D. alabastrum* (VOKES, 1976: 45), after having examined a number of the latter in the collection of the late Mr. Gordon Nowell-Usticke of St. Croix. One of his shells was figured at that time (VOKES, 1976:text-fig. 1). The Nowell-Usticke collection is now in the American Museum of Natural History.

Dermomurex (Dermomurex) gunteri
E. H. Vokes, spec. nov.

(Figures 15, 16)

Description: Shell elongate, with eight teleoconch whorls; protoconch unknown (protoconch and several early whorls

usually truncated and plugged). On early postnuclear whorls spiral ornamentation confined to a few faint spiral threads, best seen with intritacalx partially worn away; on median whorls gradually developing two, and then three, wide flattened bands, each with a series of nodules at regular intervals, approximately 0.5 mm apart; made conspicuous by the intritacalx usually being worn from the tops of the nodules, giving a dotted appearance to the shell. On body whorl five such bands, becoming less distinct with adult growth; three spiral threads between each pair of wider bands; that band at the base of the body whorl (the one covered by successive whorls) much heavier and less distinctly nodulose. Axial ornamentation on early postnuclear whorls of six angulate ridges, each placed abaperturally to corresponding varix on preceding whorl, giving a backward spiral aspect to the varical line from apex to canal. Varices initially narrow and flaring, six per whorl until about sixth postnuclear whorl, then two of every three gradually reduced in size, leaving a large, flattened buttress across the suture to mark their former position, as well as a slight flare along the siphonal canal; the other two persisting, on opposite sides of the whorl, as weak varices, only that at the aperture having any strength at all. Suture impressed, divided by the varical buttresses into a series of six deep pits per whorl. Aperture large, oval; inner lip with a wide, thickened inductura, free-standing and swept back over the parietal area at the anterior portion, appressed at the posterior end; outer lip with a rounded, sinuated edge, inner side patulous on anterior half, with about six small denticles within. Siphonal canal short, broad, recurved distally; almost closed but open by a narrow slit, with the two sides of the apertural lips almost meeting across the opening, giving the appearance of a circular parietal shield. Color of shell basically a transparent white, but usually totally covered by an extremely thick, cream-colored intritacalx; interior of aperture enameled in a pale yellow, with the tips of denticles touched by a small orange dot. Intritacalx when fresh rather massive and unornamented, but when worn, exhibiting a series of reticulated tunnels. Operculum and radula unknown.

Holotype: USNM 838035.

Dimensions of holotype: Height 20.0 mm, diameter 8.4 mm.

Type locality: Los Buzos, Combutal, Azuero Peninsula, Panamá (approximately 7°15'N, 80°30'W), John Gunter Coll.

Paratype: USNM 838036; height 15.3 mm, diameter 7.0 mm; locality same as holotype.

Discussion: During a visit to Panamá I was given 16 specimens of a *Dermomurex* so totally different from all described species there could be no question but that it was new. Although its generic affinities are unmistakable, there is no other living species with which it may be com-

pared. The most conspicuous features include the large flared aperture, in which the inductura is flattened so as to look more like a *Phyllocoma* than a *Dermomurex*, and the rows of nodules ornamenting the spiral bands. This latter ornament is also seen in the French Miocene species *D. tenellus* (Mayer) (figured in VOKES, 1975:pl. 2, figs. 1, 2), which is the only form that bears more than a generic resemblance to *D. gunteri*. In the French species there is also the tendency to develop only two varices on the adult body whorl, but it lacks the flaring inductura and the very deep pits along the sutural line. If *D. tenellus* is ancestral to *D. gunteri* there should be some connecting forms somewhere between the French Miocene and the Recent eastern Pacific, but so far these have not been found.

The entire type lot was collected by John Gunter, of Panamá City, Panamá. All were inhabited by hermit crabs on a rocky shore. But it is evident from the fact that every specimen has a damaged spire, *which was plugged in life*, that the species lives in a relatively high energy environment, presumably among the same rocks, in the wave zone.

Subgenus *Gracilimurex* Thiele, 1929

Gracilimurex THIELE, 1929:289.

Type-species: *Murex bicolor* Thiele, by original designation [*Murex bicolor* Thiele, 1929, *non Murex bicolor* Risso, 1826, =*Aspella bakeri* Hertlein & Strong, 1951].

Dermomurex (Gracilimurex) bakeri (Hertlein & Strong, 1951)

(Figures 8, 9)

Murex (Gracilimurex) bicolor THIELE, 1929:289, fig. 314 (*non M. bicolor* Risso, 1826, *nec Valenciennes*, 1832, *nec Scacchi*, 1833, *nec Cantraine*, 1835, *nec Monterosato*, 1878).

Aspella bakeri HERTLEIN & STRONG, 1951:79, pl. 26, figs. 1, 2; DUSHANE & SPHON, 1968:242, pl. 35, fig. 9 (holotype).

Aspella (?*Aspella*) *bakeri* Hertlein & Strong: KEEN, 1958b:364, fig. 375.

Gracilimurex bakeri (Hertlein & Strong): D'ATTILIO & RADWIN, 1971:346, fig. 5 (intritacalx); FAIR, 1976:23, pl. 16, fig. 217.

Aspella (Gracilimurex) bakeri Hertlein & Strong: KEEN, 1971:529, fig. 1017.

Dermomurex (Gracilimurex) bakeri (Hertlein & Strong): VOKES, 1975:129.

Dermomurex bakeri (Hertlein & Strong): RADWIN & D'ATTILIO, 1976:45, pl. 1, figs. 18, 19.

Discussion: *Dermomurex bakeri* is a peculiar species, because of the tendency of the shell to have a bilateral flattening similar to that in *Aspella*. However, the nature of the ornamentation and the radula (unpublished drawing, D'Attilio *in litt.*) seem to indicate placement in *Dermomurex* rather than *Aspella*. The only other closely related form is the Atlantic cognate, *D. (Gracilimurex) elizabethae*

(McGinty) (here figured, Figure 10), which (so far as is known) is confined to Florida, the Bahamas, and Greater Antilles, in the western Atlantic. *Dermomurex bakeri* is equally limited in distribution, being known only from the Gulf of California.

Subgenus *Trialatella* Berry, 1964

Trialatella BERRY, 1964:149.

Type-species: *Trialatella cunninghamae* Berry, 1964, by original designation.

Dermomurex (Trialatella) cunninghamae (Berry, 1964)

(Figure 11)

Trialatella cunninghamae BERRY, 1964:149; FAIR, 1976:35, pl. 16, fig. 219 (holotype).

Aspella (Trialatella) cunninghamae (Berry): KEEN, 1971:529, fig. 1019 (holotype).

Dermomurex (Trialatella) cunninghamae (Berry): VOKES, 1975:130, pl. 4, fig. 4 (holotype).

Dermomurex cunninghamae (Berry): RADWIN & D'ATTILIO, 1976:45, pl. 1, fig. 20 (paratype, Berry Coll.).

Discussion: Although named as the type of a new genus, *Trialatella*, this species was placed in *Dermomurex* subgenus *Trialatella* by VOKES (1975:130) as they differ only by the expanded varices and the elongate siphonal canal. At the same time, the Recent Caribbean "*Murex*" *abyssicola* Crosse, 1865, was placed in the same subgenus. More recently PETUCH (1979:517, figs. 1-E, 1-F) has described a second species from the western Atlantic, *D. (Trialatella) oxum*, from the Abrolhos Archipelago, Brazil (here figured, Figure 12).

Petuch did not compare his new species with *Dermomurex abyssicola*, simply stating that it was "the only Atlantic *Dermomurex*" resembling the new form. There seems little doubt that the specimen figured by VOKES (1975:pl. 4, fig. 3; refigured here, Figure 13), as a possible juvenile of *D. abyssicola*, is also to be referred to *D. oxum*. Crosse's type specimen cannot be located in either the Paris Muséum d'Histoire Naturelle or the British Museum (Natural History), but J. P. Pointier, of the Paris Museum, who has been studying the fauna of Guadeloupe for some time (POINTIER *et al.*, 1982) has collected numerous examples of a *Dermomurex* that we assume is *D. abyssicola* (Figure 14), as this is the type locality for the species. He has observed (personal communication) that the animal is *never* associated with coral reefs, as PETUCH (1979) indicated for *D. oxum*, but is found on the under side of rocky ledges in about 5 m of water. However, Petuch noted that the specimens of *D. oxum* were found dead in the mud at the base of the reef, having rolled down after death. This is almost certainly the explanation for the extraordinary depth of 250 fathoms originally cited by Crosse, for it is doubtful any member of the genus lives at that depth.

This may well be the explanation for the range of depths recorded for the eastern Pacific *Dermomurex cunninghamae*, which is found in slightly deeper water than the usual *Dermomurex* s.s., from 20 to 100 m. Records indicate the form has been taken from off the coast of Mexico (Sonora—the type and AMNH 186677; Nayarit—AMNH 74162) and Pacific Panamá (Isla Cebáco—AMNH 213736; Isla Coiba—BMNH). The association with rock rather than coral suggests that *D. abyssicola* is the true cognate of *D. cunninghamae* rather than the coral-associated *D. oxum*.

In addition to the still extant *Dermomurex abyssicola* and *D. oxum*, there are several fossil species of *Triatella* in the western Atlantic. The writer earlier (VOKES, 1975) described *D. farleyensis*, from the early Miocene Chipola Formation of northwestern Florida, and *D. antecessor*, from the Pleistocene Moin and Bermont formations of Costa Rica and Florida, respectively. In another paper (VOKES, in press A) a fourth species is described from the Miocene Cercado/Gurabo Formation of the Dominican Republic that seems to connect the younger and older fossil forms. All of these are extremely similar to the eastern Pacific *D. cunninghamae* and it seems obvious the entire group is very closely related.

Subgenus *Takia* Kuroda, 1953

Takia KURODA, 1953:190.

Type-species: *Murex inermis* Sowerby, 1841, by original designation (*non Murex inermis* Philippi, 1836, *nec M. inermis* Dujardin, 1837 [? = Philippi] = *Dermomurex (Takia) infrons* Vokes, 1974).

Dermomurex (Takia) myrakeenae
(Emerson & D'Attilio, 1970)

(Figure 17)

Aspella (Dermomurex) perplexa KEEN, 1958b:248, in part, pl. 30, figs. 12, 13, only.

Aspella myrakeenae EMERSON & D'ATTILIO, 1970:89, figs. 1, 2, 4–6, 10 (operculum), 11 (radula).

Aspella (Dermomurex) myrakeenae Emerson & D'Attilio: KEEN, 1971:527, fig. 1015 (holotype).

Dermomurex (Takia) myrakeenae (Emerson & D'Attilio): VOKES, 1975:130, pl. 5, fig. 7.

Dermomurex myrakeenae (Emerson & D'Attilio): RADWIN & D'ATTILIO, 1976:46, pl. 1, fig. 28.

Takia myrakeenae (Emerson & D'Attilio): FAIR, 1976:61, pl. 16, fig. 220.

Discussion: When the genus *Dermomurex* was treated by VOKES (1975) it was noted that *D. myrakeenae* was most closely related to the Indo-Pacific type of the subgenus *Takia*. Only in the Oligocene do we find any other New World species having an appearance much like that of the eastern Pacific form. The Miocene species referred by VOKES (1975:152–156) to the subgenus *Viator* (*D. sexangulus*, *D. vaughani*, *D. curviductus*, and *D. taurinensis*) have been removed from the latter subgenus due to the discovery of several Australian Tertiary species that change

ideas concerning evolution of the lineage (VOKES, in press B). Although they are now considered better placed in *Takia* they are probably not in a direct line from the Oligocene *D. cookei* Vokes to the Recent *D. myrakeenae*, but represent another parallel lineage. However, in the interval since 1975 there have been no other fossil species discovered that shed any light on the connection between the Oligocene and the Recent form.

This species is another of the relatively shallow-water members of *Dermomurex*, being found in depths of from 3 to 20 m, only on the west coast of Mexico, from Cabo San Lucas and Mazatlán, south to Acapulco.

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Supplementary Locality Data for Figured Specimens

The following are Tulane University Recent locality numbers:

R-98. R/V *Anton Bruun* Cruise 10, dredged in 40 m, northwest of Holandes Cay, and east-northeast of Cape San Blas (9°37'N, 78°50'W), Panamá.

R-166. Barra de Navidad, rocky point across inlet from main sand bar, Jalisco, Mexico.

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A Distributional List with Range Extensions of the Opisthobranch Gastropods of Alaska

by

RICHARD S. LEE

University of Alaska, Juneau, Alaska 99801

AND

NORA R. FOSTER

Aquatic Collection, University of Alaska Museum, Fairbanks, Alaska 99701

Abstract. The geographic occurrence of opisthobranch gastropods in the nearshore waters of Alaska is documented. Scientific names, ranges, and new observations by the authors are presented for 82 species. Eleven records represent range extensions in the North Pacific.

INTRODUCTION

FEW STUDIES HAVE been done on opisthobranch gastropods in Alaskan waters since the early work of DALL (1871) and BERGH (1879, 1880). Sporadic collecting and observations in southern Alaska have extended northward and westward the known ranges of several species formerly listed for the California, Oregon, Washington, and British Columbia coasts (ROBILLIARD, 1974; ROBILLIARD & BARR, 1978; MILLEN, 1983). In the Arctic, MACGINITIE (1959) noted the presence of several species near Point Barrow. Two recent guides to the opisthobranchs of the northeastern Pacific (MACDONALD & NYBAKKEN, 1980; BEHRENS, 1980) contain descriptions and color photographs of many of the species that may be found as far north as Prince William Sound (61°N latitude) and as far west as the Aleutian Islands. However, observations, collections, and photographs by both of the present authors have confirmed that for many species the northern and western ranges are more extensive than previously noted.

This paper presents a summary of geographic distribution data for the opisthobranch gastropods known to inhabit the nearshore waters of Alaska. The listing of families follows the order in which they are arranged in KEEN & COAN (1974). Genera and species are in alphabetical order. Observations by Richard S. Lee are indicated as (RSL); observations by Nora R. Foster, as (NRF); specimens in the Aquatic Collection, University of Alaska Museum, are indicated by (UAM). The 10 species that

are known only from the type specimens and original descriptions are indicated by an asterisk (*); a dagger (†) marks range extensions.

Order CEPHALASPIDEA

Family ACTEONIDAE

Rictaxis punctocaelatus (Carpenter, 1864)

Range: Ketchikan, Alaska to Magdalena Bay, Baja California (DALL, 1921).

Alaskan records: Ketchikan (BEHRENS, 1980); south-east Alaska—not specified (BAXTER, 1983).

Family ATYIDAE

Haminoea vesicula (Gould, 1885)

Range: Prince William Sound, Alaska to Magdalena Bay, Gulf of California (BEHRENS, 1980).

Alaskan records: Ketchikan (BEHRENS, 1980); Drier Bay, Prince William Sound (EYERDAM, 1924); Stephens Passage; Zaikof Bay, Prince William Sound; Drier Bay, Prince William Sound (UAM).

Remarks: 6 specimens from UAM were examined. Uncommon in grab samples nearshore from 30 to 50 m depth.

Haminoea virescens (Sowerby, 1833)

Range: Prince William Sound, Alaska (BEHRENS, 1980) to Mazatlán, Baja California (MARCUS, 1961).

Alaskan records: Alaska—not specified (BEHRENS,

1980); Prince William Sound (R. Rosenthal, personal communication).

Family RETUSIDAE

Retusa obtusa (Montagu, 1803)

Range: boreal Atlantic (THOMPSON & BROWN, 1976); southern Bering Sea (KRAUSE, 1885).

Alaskan records: southern Bering Sea; near St. Lawrence Island; (UAM) eastern Bering Sea (BAXTER, 1983); St. Matthew Island (KRAUSE, 1885).

Remarks: 18 specimens from UAM were examined. Common in grab samples from 30 to 100 m depth.

Retusa pertenuis Mighels, 1843

Range: Arctic Ocean; Bering Sea (KRAUSE, 1885); Prince William Sound, Alaska (EYERDAM, 1924).

Alaskan records: Hinchinbrook Island, Prince William Sound (EYERDAM, 1924); north of Akutan Pass, Aleutian Islands (KRAUSE, 1885).

Retusa semen (Reeve, 1856)

Range: Arctic and North Atlantic—not specified (LA ROCQUE, 1953); Point Collinson, Alaska (DALL, 1919); Prince William Sound, Alaska (EYERDAM, 1924).

Alaskan records: off Point Collinson (DALL, 1919); Prince William Sound (EYERDAM, 1924).

Retusa umbilicata (Montagu, 1803)

Range: North Atlantic Arctic (MACGINITIE, 1959) to Prince William Sound, Alaska (BAXTER, 1983).

Alaskan records: Prince William Sound (BAXTER, 1983); *R. cf. R. umbilicata*, southern Bering Sea (UAM).

Remarks: 2 specimens from UAM were examined.

Family DIAPHANIDAE

Diaphana brunnea Dall, 1919

Range: Kodiak Island, Alaska (DALL, 1919) to Vancouver Island and Strait of Georgia, British Columbia (COWAN, 1964).

Alaskan records: Japonski Island (UAM); Kodiak Island (type locality).

Remarks: 2 specimens from UAM were examined. Uncommon in the intertidal.

Diaphana minuta (Brown, 1827)

Range: Arctic and boreal Atlantic; Point Barrow, Alaska (MACGINITIE, 1959) to the northwestern Gulf of Alaska (BAXTER, 1983).

Alaskan records: Kenai Peninsula; Cook Inlet; northwestern Gulf of Alaska (BAXTER, 1983); Bering Sea (LEMICHE, 1941); Point Barrow (MACGINITIE, 1959).

Family PHILINIDAE

Philine polaris (Aurivillius, 1885)

Range: Arctic seas to Nanaimo, British Columbia (DALL, 1921).

Alaskan records: Prince William Sound to the Aleutian Islands (BAXTER, 1983).

Philine sinuata Stimpson, 1850

Range: northwest Atlantic (LA ROCQUE, 1953); Port Clarence, Bering Strait, Alaska (Krause in DALL, 1921).

Alaskan records: Port Clarence, Bering Strait (Krause in DALL, 1921).

Family AGLAJIDAE

Aglaja ocelligera (Bergh, 1894)

Range: Cook Inlet, Alaska (BAXTER, 1983) to Santa Barbara, California (BEHRENS, 1980).

Alaskan records: Kenai Peninsula; Cook Inlet (BAXTER, 1983); Sitka (type locality).

Melanochlamys diomedea (Bergh, 1894)

Range: Shumagin Islands, Alaska (BERGH, 1894) to Newport Bay, California (BEHRENS, 1980).

Alaskan records: to Prince William Sound and the Kenai Peninsula (BAXTER, 1983); Prince William Sound (UAM); Kodiak Island; Shumagin Islands (BERGH, 1894).

Remarks: 5 specimens from UAM were examined. Uncommon in samples from mud or sandy intertidal habitats.

Family GASTROPTERIDAE

Gastropteron pacificum Bergh, 1894

Range: Unalaska Island, Alaska to San Diego, California.

Alaskan records: lower Cook Inlet; Port Valdez (UAM); Unalaska (type locality).

Remarks: 5 lots from UAM were examined.

Family SCAPHANDRIDAE

Acteocina oldroydi Dall, 1925

Range: Cook Inlet, Alaska (BAXTER, 1983) to British Columbia (DALL, 1925).

Alaskan records: Olsen Bay, Prince William Sound; Orca Inlet, Prince William Sound; Port Valdez (UAM); Kenai Peninsula and Cook Inlet (BAXTER, 1983).

Remarks: 5 specimens from UAM were examined.

Cylichna alba (Brown, 1827)

Range: circumboreal to Monterey, California (DALL, 1921).

Alaskan records: Turner Bay, Icy Strait; Prince William Sound; Bristol Bay; Norton Sound; near Point Barrow (UAM); north of Akutan Pass, Aleutian Islands (KRAUSE, 1885).

Remarks: 31 specimens from UAM were examined. Very common in samples from 7 to 150 m.

Cylichna attonsa Carpenter, 1865

Range: eastern Bering Sea (BAXTER, 1983) to Baja California (LA ROCQUE, 1953).

Alaskan records: Gulf of Alaska (UAM); Afognak Island (EYERDAM, 1960); eastern Bering Sea (BAXTER, 1983).

Remarks: 1 specimen from UAM was examined.

Cylichna occulta Mighels, 1841

Range: Arctic and northwest Atlantic (LEMCHE, 1941); Pt. Barrow, Alaska (MACGINITIE, 1959) to Afognak Island, Alaska (EYERDAM, 1960).

Alaskan records: near Cordova; Bering Sea; Simpson Lagoon; Colville River Delta (UAM); Afognak Island (EYERDAM, 1960).

Remarks: 7 specimens from UAM were examined.

Cylichnella culcitella Gould, 1853

Range: Kodiak Island, Alaska to San Ignacio Lagoon, Baja California (BEHRENS, 1980).

Alaskan records: Kodiak Island (EYERDAM, 1960); Prince William Sound; Kenai Peninsula (BAXTER, 1983).

Cylichnella harpa Dall, 1871

Range: Kenai Peninsula and Cook Inlet, Alaska (BAXTER, 1983) to San Geronimo Island, Baja California (BEHRENS, 1980).

Alaskan records: Prince William Sound; Kenai Peninsula (BAXTER, 1983); *C. cf. C. harpa*, Bering Sea near St. Lawrence Island (UAM).

Remarks: 2 specimens from UAM were examined.

**Scaphander willetti* Dall, 1919

Known only from the type specimen collected at Forrester Island, Alaska.

Order NOTOASPIDAE

Family PLEUROBRANCHIDAE

†*Berthella denticulatus* (MacFarland, 1966)

Range: Point Craven, Alaska to Point Pinos, Pacific Grove, California (LAMBERT, 1976).

Alaskan records: Point Craven (RSL); Hole-in-the-Wall, Prince of Wales Island (UAM); Baranof Island (BARR & BARR, 1983).

Remarks: Range extension from Baranof Island (BARR & BARR, 1983). Two specimens from UAM were examined, both from the shallow nearshore subtidal (3 m). Specimens from Point Craven had external cyclopoid copepod parasites tentatively identified as *Anthesius obtusispina* Ho, 1983.

Berthella sideralis (Loven, 1847)

Range: Norwegian coast (Odhner, 1939 in MACFARLAND, 1966) to Unalaska Island, Alaska (Bergh, 1898 in MACFARLAND, 1966).

Alaskan records: Unalaska Island, Aleutians (Bergh, 1898 in MACFARLAND, 1966).

Order NUDIBRANCHIA

Family ALDISIDAE

Aldisa cooperi Robilliard & Baba, 1972

Range: Hogan Island, Alaska to Trinidad Head, California (MILLEN, 1983).

Alaskan records: Sam Sing Cove (RSL); Hogan Island (MILLEN, 1983).

Remarks: observed in the intertidal.

Aldisa zetlandica (Alder & Hancock, 1855)

Range: North Atlantic; Pt. Barrow, Alaska (MACGINITIE, 1959).

Alaskan records: Point Barrow (MACGINITIE, 1959).

Family ARCHIDORIDAE

Archidoris montereyensis (Cooper, 1863)

Range: Kachemak Bay, Alaska (ROSENTHAL & LEES, 1976) to San Diego, California (ROBILLIARD, 1974).

Alaskan records: Port Valdez (ROBILLIARD, 1974); Sitka (BERGH, 1878); Seldovia (RSL); Kalinin Bay (RSL); Spruce Island (NRF); Kachemak Bay (ROSENTHAL & LEES, 1976).

Remarks: common in the intertidal.

Archidoris odhneri (MacFarland, 1966)

Range: Kenai Peninsula, Alaska (ROBILLIARD & BARR, 1978) to Point Loma, San Diego County, California (ROBILLIARD, 1974).

Alaskan records: Port Dick (ROBILLIARD & BARR, 1978); Auke Bay (ROBILLIARD, 1974); Humpy Cove, Resurrection Bay (NRF); Three Entrance Bay; Sam Sing Cove (RSL).

Remarks: observed in the intertidal and shallow subtidal.

Family ROSTANGIDAE

†*Rostanga pulchra* MacFarland, 1905

Range: Point Craven, Alaska to Bahia de los Angeles, Gulf of California (LANCE, 1966); Chile (MARCUS, 1961); Argentina (Marcus & Marcus, 1966 in McDONALD, 1983).

Alaskan records: Three Entrance Bay; Sam Sing Cove; Kalinin Bay; Point Craven (RSL); Big Branch Rock (R. Rosenthal, personal communication).

Remarks: range extension from Dundas Island, British Columbia (LAMBERT, 1976). Common in the intertidal.

Family CADLINIDAE

Cadlina luteomarginata MacFarland, 1966

Range: Lynn Canal, Alaska (ROBILLIARD & BARR, 1978) to Punta San Eugenio, Baja California (LANCE, 1961).

Alaskan records: Point Therese, Point Lena, and Amalga Harbor, Lynn Canal (ROBILLIARD & BARR, 1978); Three Entrance Bay; Sam Sing Cove; Halibut Point (RSL).

Remarks: common in the intertidal.

†*Cadlina modesta* MacFarland, 1966

Range: Point Lena, Alaska to La Jolla, California (MACFARLAND, 1966).

Alaskan records: Three Entrance Bay; Point Craven; Point Lena (RSL).

Remarks: range extension from Vancouver Island, British Columbia (ROBILLIARD, 1971).

Cadlina pacifica Bergh, 1879

Range: Captain's Bay, Unalaska Island, Alaska to Coal Harbor, Shumagin Islands, Alaska (BERGH, 1879).

Alaskan records: Captain's Bay, Unalaska Island; Coal Harbor, Shumagin Islands (BERGH, 1879).

Family DISCODORIDAE

†*Anisodoris lentiginosa* Millen, 1983

Range: Kenai Peninsula, Alaska; Strait of Georgia, British Columbia (MILLEN, 1983).

Alaskan records: Gulf of Alaska (59°21.2'N, 150°28.4'W) (UAM).

Remarks: range extension from Queen Charlotte Strait, British Columbia (MILLEN, 1983). One specimen from UAM was examined.

†*Anisodoris nobilis* (MacFarland, 1905)

Range: Kodiak Island, Alaska to Baja California (FARMER & COLLIER, 1963).

Alaskan records: Annette Island; Kalinin Bay; Seldovia; Women's Bay, Kodiak Island (RSL); Washington Bay, Kuiu Island (EYERDAM, 1977); Spruce Island (UAM).

Remarks: range extension from Kuiu Island (EYERDAM, 1977). Uncommon in the intertidal. One specimen from UAM was examined.

Discodoris sandiegensis Cooper, 1863

Range: Unalaska Island, Alaska (BERGH, 1894) to Cabo San Lucas, Baja California, Mexico (LANCE, 1961); Japan (BABA, 1957).

Alaskan records: Sam Sing Cove; Kalinin Bay; Women's Bay, Kodiak Island (RSL); Peratrovich Island (UAM); Unalaska (BERGH, 1894); Naked Island, Prince William Sound; Kachemak Bay (ROSENTHAL & LEES, 1976).

Remarks: 2 specimens from UAM were examined. Common in the intertidal.

Family CALYCIDORIDIDAE

Calycidoris guentheri Abraham, 1876

Range: Arctic seas; Bering Strait, Alaska (ROGINSKAYA, 1972).

Alaskan records: Bering Strait (ROGINSKAYA, 1972) near Wainwright; near Pingok Island; Harrison Bay (UAM).

Remarks: 6 lots from UAM were examined. Uncommon in samples from 14 to 44 m.

Family POLYCEMATIDAE

**Issena pacifica* Iredale & O'Donoghue, 1923

Known only from the type specimen collected at Unimak Island, Alaska.

**Palio pallida* Bergh, 1880

Known only from the type specimen collected at Kiska Harbor, Alaska.

Family TRIOPHIDAE

Triopha catalinae (Cooper, 1863)

Range: Amchitka Island, Alaska (ROBILLIARD, 1974) to El Tomatal, Baja California (BERTSCH & ROSAS, 1984); Japan (BABA, 1957).

Alaskan records: Shumagin Islands (BERGH, 1880); Stephens Passage (BARR & BARR, 1983); Port Walter, Baranof Island; Amchitka Island (ROBILLIARD, 1974); Point Craven; Three Entrance Bay (RSL); Sunny Cove, Spruce Island (NRF); Bluff Point, Kachemak Bay; Prince William Sound (ROSENTHAL & LEES, 1976).

Remarks: commonly observed in the intertidal and subtidal (3 m).

Family ONCHIDORIDAE

**Acanthodoris caerulea* Bergh, 1880

Known only from the type specimen collected at the north end of Nunivak Island, Alaska.

†*Acanthodoris hudsoni* MacFarland, 1905

Range: Three Entrance Bay, Alaska to Gaviota, Santa Barbara County, California (LEE & BROPHY, 1969).

Alaskan records: Three Entrance Bay (RSL).

Remarks: range extension from Porcher Island, British Columbia (LAMBERT, 1976). Occasionally observed in the intertidal.

†*Acanthodoris nanaimoensis* O'Donoghue, 1921

Range: Halibut Point, Baranof Island, Alaska to Purissima Point, Santa Barbara County, California (LEE & BROPHY, 1969).

Alaskan records: Three Entrance Bay; Halibut Point (RSL).

Remarks: range extension from Wales Island, British Columbia (LAMBERT, 1975). Commonly observed in the intertidal.

Two color forms have been photographed in Sitka waters. The more common is light gray to white in body color with yellow-tipped papillae. The other form is brown to brownish gray with the yellow tips of the papillae standing out in strong contrast (RSL).

Acanthodoris pilosa (Abildgaard, 1789)

Range: circumboreal; Kiska Island, Alaska (BERGH, 1880) to Morro Bay, San Luis Obispo County, California (MCDONALD, 1983).

Alaskan records: Kiska Island; Unalaska Island; Yukon Harbor, Shumagin Islands (BERGH, 1880); Uyak Bay, Kodiak Island (UAM); Kenai Peninsula; Cook Inlet (BAXTER, 1983); Zaikof Bay, Prince William Sound (ROSENTHAL, personal communication).

Remarks: 2 lots from UAM were examined.

**Adalaria albopapillosa* (Dall, 1871)

Known only from the type specimen collected at Sitka Harbor, Alaska.

Adalaria pacifica Bergh, 1880

Range: Pribilof Islands, Alaska to Victoria, British Columbia (MILLEN, 1983).

Alaskan records: Bering Sea, northwest of the Pribilof Islands (UAM).

Remarks: 2 lots from UAM were examined.

**Adalaria tschuktschica* Krause, 1885

Known only from the type specimen collected at "Metshigme Bay," Bering Sea.

**Adalaria virescens* Bergh, 1880

Known only from the type specimen collected at Unalaska Island, Alaska.

**Akiodoris lutescens* Bergh, 1880

Range: Aleutian Islands (BERGH, 1880).

Alaskan records: Nazan Bay, Atka Island; Kiska Harbor; Unalaska Island (BERGH, 1880).

Onchidoris bilamellata (Linnaeus, 1767)

Range: circumboreal; Hagemeister Island, Alaska (THOMPSON & BROWN, 1976) to Morro Bay, San Luis Obispo County, California (McDONALD, 1970).

Alaskan records: Kiska Island, Aleutians (BERGH, 1894); Hagemeister Island; Sandborn Harbor, Shumagin Islands (BERGH, 1880); Spruce Island (NRF); Berners Bay; Juneau; Kalinin Bay; Point Craven; Point Courverden (RSL); Nikishka Beach, Kenai Peninsula (UAM); Kachemak Bay (ROSENTHAL & LEES, 1976).

Remarks: 4 lots from UAM were examined. Very common in the upper intertidal.

Onchidoris hystricina (Bergh, 1880)

Range: south of Cabo Colinet, Baja California (FARMER, 1967) to Kiska Island, Alaska (BERGH, 1880).

Alaskan records: Washington Bay (EYERDAM, 1979); Kiska Island (BERGH, 1880); Three Entrance Bay (RSL).

Remarks: not common. Observed once in the intertidal.

Onchidoris varians (Bergh, 1878)

Range: Aleutian Islands, Alaska (BERGH, 1878); Washington Bay, Kuiu Island, Alaska (EYERDAM, 1977).

Alaskan records: Kiska Island; Unalaska Island (BERGH, 1878); Washington Bay (EYERDAM, 1977).

Family CORAMBIDAE

†*Corambe pacifica* MacFarland & O'Donoghue, 1929

Range: Punta San Eugenio, Baja California (McDONALD, 1983) to Sitka, Alaska.

Alaskan records: Sam Sing Cove (RSL); Ataku Island (R. Rosenthal, personal communication).

Remarks: range extension from Nanaimo, British Columbia (McDONALD, 1983).

Family TETHYIDAE

Melibe leonina (Gould, 1852)

Range: Kodiak Island, Alaska (EYERDAM, 1960) to Punta Abreojos, Baja California (LANCE, 1966).

Alaskan records: Dall Island (O'DONOGHUE, 1926); Three Entrance Bay; Sam Sing Cove (RSL); Still Harbor, Baranof Island (UAM); Neets Bay (BARR & BARR, 1983); Kodiak Island (EYERDAM, 1960); Kenai Peninsula; Cook Inlet (BAXTER, 1983); Port Gravina, Prince William Sound (ROSENTHAL, 1977).

Remarks: 2 specimens from UAM were examined. Common in the low intertidal and shallow subtidal.

Family DENDRONOTIDAE

Dendronotus albus MacFarland, 1966

Range: Kenai Peninsula, Alaska (ROBILLIARD & BARR, 1978) to Coronado Islands, Baja California (ROBILLIARD, 1970).

Alaskan records: Port Dick, Kenai Peninsula (ROBILLIARD & BARR, 1978).

Dendronotus dalli Bergh, 1879

Range: circumboreal; Bering Strait, Alaska to Puget Sound, Washington (ROBILLIARD, 1970).

Alaskan records: Bering Strait (BERGH, 1879); Bering Sea and Unalaska Island (MACFARLAND, 1966); South Shelter Island (ROBILLIARD, 1974); southeast Bering Sea (UAM).

Remarks: 5 lots from UAM were examined. Common in samples from 50 to 100 m. Observed in the intertidal in southeast Alaska.

Dendronotus frondosus (Ascanius, 1774)

Range: Arctic seas (THOMPSON & BROWN, 1976); circumboreal; Point Barrow, Alaska to southern California (ROBILLIARD, 1970).

Alaskan records: Point Barrow (MACGINITIE, 1959); Port Moller (BERGH, 1879); Hagemeister Island (MACFARLAND, 1966); St. Lawrence Island (KRAUSE, 1885); Kalinin Bay (RSL); Norton Sound, western Beaufort Sea; northeast Chukchi Sea (UAM).

Remarks: 10 lots from UAM were examined. Common in samples from 50 to 100 m.

Dendronotus iris Cooper, 1863

Range: Unalaska Island, Alaska to Coronado Island, Baja California (ROBILLIARD, 1970).

Alaskan records: frequent records from the subtidal waters throughout the state (ROBILLIARD, 1970); off Unalaska Island (ROBILLIARD, 1970); Steamer Bay (BARR & BARR, 1983).

Dendronotus robustus (Verrill, 1870)

Range: eastern Chukchi Sea; Beaufort Sea; Arctic and North Atlantic oceans (ROBILLIARD, 1970).

Alaskan records: western Beaufort Sea (71°35.4'N, 153°40.1'W); eastern Chukchi Sea (71°35'N, 163°58'W; 71°05'N, 160°08'W).

Remarks: 3 lots from UAM were examined. Uncommon in samples from 46 to 62 m.

Dendronotus rufus O'Donoghue, 1921

Range: Auke Bay, Alaska (ROBILLIARD, 1974) to Seattle, Washington (ROBILLIARD, 1970).

Alaskan records: Auke Bay (ROBILLIARD, 1974); Stephens Passage (BARR & BARR, 1983).

Family TRITONIIDAE

Tochuina tetraquetra (Pallas, 1788)

Range: Kuril Islands; Unalaska Island, Alaska (BERGH, 1884) to Catalina Island, California (ROBILLIARD, 1974).

Alaskan records: Unalaska Island (BERGH, 1884); Resurrection Bay; northeast Gulf of Alaska (UAM); Sam Sing Cove; Kalinin Bay (RSL); Naked Island, Prince William Sound (ROSENTHAL & LEES, 1982).

Remarks: common in samples from the northeast Gulf of Alaska. Observed in the subtidal to 10 m in southeast Alaska.

Tritonia diomedea Bergh, 1894

Range: Shumagin Islands, Alaska (BERGH, 1894) to Panama; Okhotsk Sea; Japan; Florida (MCDONALD, 1983).

Alaskan records: Shumagin Islands (BERGH, 1894); northeast Gulf of Alaska; Prince William Sound (UAM); Sam Sing Cove (RSL).

Remarks: 17 lots from UAM were examined. Common in samples from the northeast Gulf of Alaska. Observed to 10 m in southeast Alaska.

Tritonia festiva (Stearns, 1873)

Range: Kachemak Bay, Alaska (ROSENTHAL & LEES, 1976) to Los Coronados Islands, Baja California (LANCE, 1961); Japan (MCDONALD, 1983).

Alaskan records: Port Dick, Kenai Peninsula (ROBILLIARD & BARR, 1978); Steamer Bay (BARR & BARR, 1983); Sam Sing Cove (RSL); Kachemak Bay (ROSENTHAL & LEES, 1976); Danger Island, Prince William Sound (R. Rosenthal, personal communication).

Remarks: commonly observed in the subtidal to 10 m.

Family ARMINIDAE

†*Armina californica* (Cooper, 1863)

Range: Kayak Island, Gulf of Alaska to Panama (BERGH, 1894).

Alaskan records: near Kayak Island, Gulf of Alaska (UAM); Ernest Sound (D. Kowalski, personal communication); Slocum Arm (BARR & BARR, 1983).

Remarks: range extension from Slocum Arm, Chichagof Island (BARR & BARR, 1983). One UAM specimen was examined. Uncommon in the subtidal.

Family ZEPHYRINIDAE

Antiopella barbarensis (Cooper, 1863)

Range: Klu Bay, Revillagigedo Island, Alaska (ROBIL-

LIARD & BARR, 1978) to Baja California and the Gulf of California (MCDONALD, 1983).

Alaskan records: Klu Bay (ROBILLIARD & BARR, 1978).

Family DIRONIDAE

†*Dirona albolineata* (Eliot, 1905)

Range: Kachemak Bay, Alaska to La Jolla, California (LANCE, 1966).

Alaskan records: Quiet Harbor (BARR & BARR, 1983); Three Entrance Bay; Sam Sing Cove (RSL); Bidarka Point, Prince William Sound; Kachemak Bay (R. Rosenthal, personal communication).

Remarks: range extension from Quiet Harbor, Etolin Island, Alaska (BARR & BARR, 1983). Common in the intertidal near Sitka.

Three color phases exist, the most common being white in background. The next most frequent is a grayish-pink; and the third, a clear light brick-red to pink form (RSL).

Dirona aurantia Hurst, 1966

Range: King Island, Norton Sound, Alaska (ROBILLIARD & BARR, 1978) to Puget Sound, Washington (ROBILLIARD, 1974).

Alaskan records: King Island; Pribilof Island; Unimak Pass (ROBILLIARD & BARR, 1978); Stikine Pass (BARR & BARR, 1983); Point Therese; Port Valdez (ROBILLIARD, 1974); Women's Bay; Point Craven (RSL); Kachemak Bay (R. Rosenthal, personal communication).

Remarks: commonly observed in the intertidal and subtidal.

Family CORYPHELLIDAE

Flabellina fusca (O'Donoghue, 1921)

Range: Port Valdez, Alaska (ROBILLIARD, 1974) to Seal Rocks State Park, Oregon (ROBILLIARD, 1974).

Alaskan records: Auke Bay; Point Therese; Port Valdez (ROBILLIARD, 1974); Point Craven (RSL); Tenakee Inlet (BARR & BARR, 1983).

Flabellina salmonacea (Couthouy, 1838)

Range: Arctic circumboreal (MACGINITIE, 1959); Point Barrow, Alaska to Pender Harbor, British Columbia (MILLEN, 1983).

Alaskan records: Point Barrow (MACGINITIE, 1959); Bering Strait (LEMICHE, 1941).

**Flabellina subrosacea* (Eschscholtz, 1831)

Known only from the type specimen collected near Sitka.

Flabellina trilineata (O'Donoghue, 1921)

Range: Lisianski Inlet, Alaska to Los Coronados Islands, Baja California (MILLEN, 1983).

Alaskan records: Lisianski Inlet (MILLEN, 1983).

**Flabellina trophina* (Bergh, 1894)

Known only from the type specimen collected at Port Althorp.

Flabellina verrucosa (Sars, 1829)

Range: circumboreal; Hogan Island, Alaska to San Juan Islands, Washington; Japan; North Atlantic (MILLEN, 1983).

Alaskan records: Hogan Island (MILLEN, 1983).

Family CUTHONIDAE

Cuthona concinna (Alder & Hancock, 1843)

Range: Lisianski Inlet, Alaska to White Rock, British Columbia; North Atlantic (MILLEN, 1983).

Alaskan records: Lisianski Inlet, Alaska (MILLEN, 1983).

Cuthona nana (Alder & Hancock, 1842)

Range: Britain; Scandinavia; Bering Sea (THOMPSON & BROWN, 1976).

Alaskan records: St. Lawrence Bay, Bering Sea (KRAUSE, 1885).

Family FIONIDAE

Fiona pinnata (Eschscholtz, 1831)

Range: pelagic in northern temperate oceans (LANCE, 1961).

Alaskan records: Sitka (type locality).

Family AEOLIDIIDAE

Aeolidia papillosa (Linnaeus, 1761)

Range: cosmopolitan in the Northern Hemisphere (MCDONALD, 1983).

Alaskan records: Chignik Bay; Sanborn Harbor, Shumagin Islands (BERGH, 1879); Tutka Bay; Izembek Lagoon (UAM); Outer Point; Sam Sing Cove; Point Craven (RSL); Kachemak Bay (ROSENTHAL & LEES, 1976); Rowan Bay (BARR & BARR, 1983).

Remarks: 2 UAM lots were examined. Uncommonly observed in the intertidal.

Family PHIDIANIDAE

†*Phidiana crassicornis* (Eschscholtz, 1831)

Range: Kodiak Island, Alaska to the Gulf of California (LANCE, 1966).

Alaskan records: Rowan Bay (BARR & BARR, 1983); Wrangell; Baranof Warm Springs Bay; Juneau; Seldovia; Seward; Kodiak (RSL); Sitka (BERGH, 1879); Port Valdez; Resurrection Bay (UAM).

Remarks: range extension from Rowan Bay, Kuiu Island, Alaska (BARR & BARR, 1983). Very commonly observed in the intertidal and subtidal (9 m).

Order GYMNOPHILA

Family ONCHIDELLIDAE

Onchidella borealis Dall, 1871

Range: Aleutian Islands, Alaska to northern California (MARCUS, 1961).

Table 1

New distribution sites of opisthobranch gastropods in Alaska.

Location	Latitude (N)	Longitude (W)
Annette Island	55°09'	131°28'
Ataku Island	56°49'45"	135°29'
Baranof Warm Springs Bay	57°05'	134°47'
Berners Bay	58°43'	135°00'
Bidarka Point, Prince William Sound	60°49'	146°37'
Big Branch Rock, Baranof Island	56°16'48"	134°50'50"
Bluff Point, Kachemak Bay	59°40'	151°41'
Colville River Delta	70°27'	150°07'
Cordova	60°33'	145°45'
Danger Island, Prince William Sound	59°55'30"	148°05'
Drier Bay, Knight Island	60°18'30"	147°52'30"
Ernest Sound	56°11'	132°18'
Halibut Point, Baranof Island	57°06'	135°24'
Hole-in-the-Wall, Prince of Wales Island	56°16'10"	133°37'
Humpy Cove, Resurrection Bay	59°58'	149°18'
Icy Strait	58°18'	134°45'
Izembek Lagoon	55°20'	162°48'
Japonski Island	57°03'	135°22'
Juneau	58°18'15"	134°24'30"
Kalinin Bay	57°20'	135°47'
Kayak Island	59°56'	144°23'
Kodiak	57°47'20"	152°47'10"
Naked Island	60°40'	147°25'
Nikishka Beach	60°45'	151°18'
Olsen Bay	60°43'20"	146°12'30"
Orca Inlet	60°31'	145°52'
Outer Point	58°18'05"	134°41'15"
Peratrovich Island	55°35'	133°06'
Pingok Island, Harrison Bay	70°31'10"	149°31'30"
Point Bridget	58°40'45"	134°59'20"
Point Courverden	58°11'25"	135°03'10"
Point Craven	57°28'	134°52'
Port Lena	58°23'45"	134°46'45"
Port Valdez	61°05'	146°39'
Sam Sing Cove	56°59'	135°21'
Seldovia	59°26'15"	151°42'30"
Simpson Lagoon	70°30'	149°12'
Spruce Island	57°55'	152°25'
Stephens Passage	57°13'	133°39'
Still Harbor, Baranof Island	56°33'30"	135°02'30"
Three Entrance Bay	56°58'40"	135°22'40"
Ugaiushak Island	56°47'	156°51'
Uyak Bay	57°48'	154°04'
Women's Bay	57°43'	152°31'
Wrangell	56°28'	132°22'40"
Zaikof Bay, Montague Island	60°19'	146°58'

Alaskan records: Tutka Bay; Spruce Island; Ugaiushak Island; Point Bridget (UAM); Pt. Craven (RSL); Kachemak Bay (ROSENTHAL & LEES, 1976).

Remarks: 8 UAM specimens were examined. Common in the upper intertidal.

DISCUSSION

It should be noted that 11 of the listed species are known only from the type specimens or original collections, some collected over 100 years ago. This lack of information may be because recent collections or recorded observations are few, or because the species in question have very limited ranges.

Major range extensions include species found farther west, *i.e.*, *Anisodoris nobilis*, and species found farther north, *i.e.*, *Armina californica*. The apparent lack of two major groups, the Sacoglossa and Aplysiomorpha, as well as the low number of Anaspidea may, likewise, reflect either a lack of collections or the absence of these orders from the Alaskan fauna.

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NOTES, INFORMATION & NEWS

California Malacozoological Society

California Malacozoological Society, Inc., is a non-profit educational corporation (Articles of Incorporation No. 463389 were filed January 6, 1964 in the office of the Secretary of State). The Society publishes a scientific quarterly, *The Veliger*. Donations to the Society are used to pay a part of the production costs and thus to keep the subscription rate at a minimum. Donors may designate the Fund to which their contribution is to be credited: Operating Fund (available for current production); Savings Fund (available only for specified purposes, such as publication of especially long and significant papers); Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

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Although we would like to publish papers without charge, high costs of publication require that we ask authors to defray a portion of the cost of publishing their papers in *The Veliger*. We wish, however, to avoid possible financial handicap to younger contributors, or others without financial means, and to have charges fall most heavily on those who can best afford them. Therefore, the following voluntary charges have been adopted by the Executive Board of the California Malacozoological Society: \$30 per printed page for authors with grant or institutional support and \$10 per page for authors who must pay from personal funds (2.5 manuscript pages produce about 1 printed page). In addition to page charges, authors of papers containing an extraordinary number of tables and figures should expect to be billed for these excess tables and figures at cost. It should be noted that even at the highest rate of \$30 per page the Society is subsidizing well over half of the publication cost of a paper. However, authors for whom the regular page charges would present a financial handicap should so state in a letter accompanying the original manuscript. The letter will be considered an application to the Society for a grant to cover necessary publication costs.

We emphasize that these are *voluntary* page charges and that they are unrelated to acceptance or rejection of manuscripts for *The Veliger*. Acceptance is entirely on the basis of merit of the manuscript, and charges are to be paid *after* publication of the manuscript, if at all. Because these contributions are voluntary, they may be considered by authors as tax deductible donations to the Society. Such contributions are necessary, however, for the continued good financial health of the Society, and thus the continued publication of *The Veliger*.

Reprints

While it was hoped at the "birth" of *The Veliger* that a modest number of reprints could be supplied to authors free of charge, this has not yet become possible. Reprints are supplied to authors at cost, and requests for reprints should be addressed directly to the authors concerned. The Society does not maintain stocks of reprints and also cannot undertake to forward requests for reprints to the author(s) concerned.

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Since the inception of the *The Veliger* in 1958, many generous people, organizations, and institutions have given our journal substantial support in the form of monetary donations, either to *The Veliger* Endowment Fund, *The Veliger* Operating Fund, or to be used at our discretion. This help has been instrumental in maintaining the high quality of the journal, especially in view of the rapidly rising costs of production.

At a recent Executive Board Meeting, we felt we should find a way to give much-deserved recognition to those past and future donors who so evidently have our best interests at heart. At the same time, we wish to broaden the basis of financial support for *The Veliger*, and thus to serve our purpose of fostering malacological research and publication. Accordingly, it was decided to publicly honor our friends and donors. Henceforth, donors of \$1000.00 or more will automatically become known as **Patrons** of *The Veliger*, donors of \$500.00 or more will be known as **Sponsors** of *The Veliger*, and those giving \$100.00 or more will become **Benefactors** of *The Veliger*. Lesser donations are also sincerely encouraged, and those donors will be known as **Friends** of *The Veliger*. As a partial expression of our gratitude, the names of donors in these different categories will be listed in a regular issue of the journal. Of course, we will honor the wishes of any donor who would like to remain anonymous. The Treasurer of the

California Malacozoological Society will provide each member of the new patronage groups with a receipt that may be used for tax purposes.

We thank all past and future donors for their truly helpful support and interest in the Society and *The Veliger*. Through that support, donors participate directly and importantly in producing a journal of high quality, one of which we all can be proud.

Subscription Rates and Membership Dues

At its regular Annual Business Meeting on October 19, 1984, the Executive Board of the California Malacozoological Society, Inc., set the subscription rates and membership dues for Volume 28 of *The Veliger*. For affiliate members of the Society, the subscription rate for Volume 28 will remain unchanged at US\$22.00; this now *includes* postage to domestic addresses. For libraries and nonmembers the subscription rate will increase very slightly to US\$44.00, also now with postage to domestic addresses included. An additional US\$3.00 is required for all subscriptions sent to foreign addresses, including Canada and Mexico.

Affiliate membership in the California Malacozoological Society is open to persons (no institutional memberships) interested in any aspect of malacology. There is a one-time membership fee of US\$2.00, after payment of which, membership is maintained in good standing by the timely renewal of the subscription.

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All back volumes still in print, both paper covered and cloth bound, will be available only from C.M.S., Inc., P.O. Box 9977, Berkeley, CA 94709. The same applies to the supplements still in print, with certain exceptions (see below). Prices of available items may be obtained by applying to the address given above.

Volumes 1 through 13 are out of print.

Supplements available from C.M.S.

Supplement to Volume 3:

[Part 1: Opisthobranch Mollusks of California by Prof. Ernst Marcus;

Part 2: The Anaspeidea of California by Prof. R. Beeman, and the Thecosomata and Gymnosomata of the California Current by Prof. John A. McGowan]

Supplement to Volume 11:

[The Biology of Acmaea by Prof. D. P. Abbott *et al.*, ed.]

Supplement to Volume 14:

[The Northwest American Tellinidae by Dr. E. V. Coan]

Supplement to Volume 16:

[The Panamic-Galapagan Epitoniidae by Mrs. Helen DuShane]

Supplement to Volume 17:

[Growth Rates, Depth Preference and Ecological Succession of Some Sessile Marine Invertebrates in Monterey Harbor by Dr. E. C. Haderlie]

Our stock of this supplement is exhausted. Copies may be obtained by applying to Dr. E. C. Haderlie, U.S. Naval Post-Graduate School, Monterey, CA 93940.

Supplements not available from C.M.S.

Supplements to Volume 7 (Glossary) and 15 (Ovulidae) are sold by 'The Shell Cabinet,' 12991 Bristow Road, Nokesville, VA 22123; supplement to Volume 18 (Chitons) is available from 'The Secretary,' Hopkins Marine Station, Pacific Grove, CA 93950.

Single Copies of THE VELIGER

We have on hand some individual copies of earlier issues of our journal and are preparing a list of the various issues available with the prices. Some issues are present in only one or two copies, while others may be present in 10 or more copies. As we are anxious to make room, we will offer these numbers at an exceptionally low price. This list may be obtained by sending a self-addressed, stamped envelope to C.M.S., Inc., Post Office Box 9977, Berkeley, CA 94709. Foreign correspondents should enclose one international postal reply coupon.

Annual Meeting

American Malacological Union

The American Malacological Union will hold its annual meeting on the campus of the University of Rhode Island on July 29–August 3, 1985. Three special symposia are planned: one on molluscan egg capsules, organized by Jan Pechenik; a second on molluscan radulae, organized by Bob Bullock and Carole Hickman; and a third on the ecology of freshwater mollusks, organized by Eileen Jokinen.

The Boston Malacological Club is planning special events in commemoration of its 75th anniversary. There will also be contributed papers, a poster session, marine and freshwater field trips, workshops, an auction to benefit the AMU Symposium Endowment Fund, exhibits, and commercial sales of items of interest to attendees, and a New England clam bake. A program to honor junior malacologists will open the meeting.

For further details write to Dr. M. R. Carriker, College of Marine Studies, University of Delaware, Lewes, DE 19958 (302-645-4274).

Annual Meeting

Western Society of Malacologists

The annual meeting of the Western Society of Malacologists will be held from August 18–21, 1985, on the campus of the University of California, Santa Barbara. The main emphasis will be the molluscan fauna of the eastern Pacific, with sessions concerning land snails, paleontology, and other topics. There will be a symposium on Hawaiian mollusks chaired by Mrs. Beatrice Burch.

Anyone interested in pre-registration or a call for pa-

pers please contact William D. Pitt, President WSM, 2444 38th Avenue, Sacramento, CA 95822 (916-428-3899, home evenings).

Notes to Prospective Authors

The increasing use of computers to prepare manuscript copy prompts the following notes. We request that the right margin of submitted papers be prepared "ragged," that is, *not* justified. Although right-justified margins on printed copy sometimes look "neater," the irregular spacing that results between words makes the reviewer's, editor's, and printer's tasks more difficult and subject to error. Similarly, the automatic hyphenation capability of many machines makes for additional editorial work and potential confusion; it is best not to hyphenate words at the end of a line. Above all, manuscripts should be printed with a printer that yields unambiguous, high-quality copy. With some printers, especially some of the dot-matrix kinds, copy is generally difficult to read and, specifically, the letters "a, p, g, and q" are difficult to distinguish, especially when underlined as for scientific names; again, errors may result.

Other reminders are (1) that three copies of everything (figures, tables, and text) should be submitted to speed the review process, and (2) absolutely everything should be double-spaced, including tables, references, and figure legends.

Because the *Veliger* is an international journal, we occasionally receive inquiries as to whether papers in languages other than English are acceptable. Our policy is that manuscripts must be in English. In addition, authors whose first language is other than English should seek the assistance of a colleague who is fluent in English *before* submitting a manuscript.

BOOKS, PERIODICALS & PAMPHLETS

Intertidal Plants and Animals of the Landels-Hill Big Creek Reserve

AVA FERGUSON (editor). 1984. Publication No. 14, Environmental Field Program, University of California, Santa Cruz. 106 pp., index map, 5 figs. \$8.00. Copies are available from the Environmental Field Program, 231 Kerr Hall, University of California, Santa Cruz, Santa Cruz, CA 95064 (\$8.00 plus \$2.00 postage and handling; checks payable to the UC Regents).

The University of California Natural Reserve System (NRS) has been built in a brief span of 20 years into the finest academic natural reserve system in North America, and perhaps the world. The system currently contains 26 reserves encompassing undisturbed samples of 106 of the state's diverse natural habitat types. The reserves function as outdoor laboratories and classrooms for researchers, students, and teachers from institutions throughout the world.

Under a cluster system of management, different reserves are administered by different campuses within the University. The system is still too young to have generated published surveys of its reserves. This volume summarizes a study conducted in 1981 at four sites along the 2.8 km shoreline of the Landels-Hill Big Creek Reserve in Monterey County on the Big Sur Coast.

The Landels-Hill Big Creek Reserve was acquired in 1977 and is one of seven reserves in the System containing marine habitats. The only other reserve in the System for which published faunal documentation is available is the Bodega Marine Reserve in Sonoma County (Standing, J. M., B. Browning & J. W. Speth. 1975. The natural resources of Bodega Harbor. Calif. State Dept. Fish & Game Coastal Wetlands Series No. 11, 181 pp., 13 pls., 7 appendices). The Bodega Marine Laboratory and research interest in Bodega harbor predate the Reserve System, so it is not surprising that the fauna is better known. How-

ever, even the Standing report is not well known or widely distributed. It is for this reason that I have chosen to preface this review with some background information on the Natural Reserve System.

The Big Creek Reserve is important because it lies within the poorly understood transition between the temperate Oregonian Marine Province and the warm temperate Californian Marine Province. In addition to its biologically unexplored characteristics as a transition zone, this segment of coast stands as a relatively remote and isolated region between two of the most densely urbanized and disturbed segments of the California Coast. Heavy wave impact and exposures of greenstone (a substrate of unusual properties) may help account for the relatively simple intertidal communities, although they have a number of notable aspects, including one of the few undisturbed California mainland populations of the large owl limpet, *Lottia gigantea*.

This volume documents, with annotated lists, 88 species of algae, 2 marine vascular plants, and 192 species of invertebrates (55 mollusks) and provides an excellent overview of the intertidal zonation, the community ecology, and the provincial affinities and unique features of the marine flora and fauna.

What is most remarkable is that this volume is the result of the work of an undergraduate biology class at U.C. Santa Cruz, taught by David R. Lindberg, assisted by Douglas J. Eernisse, and Chet Chaffee. It was assembled from a combination of their efforts and compilation and editing of student reports. The level of student contribution is impressive, including some highly professional drawings and spectacular photographs. The publication will serve not only as an invaluable reference for future research on this remote stretch of coastline in the transition zone, but it will provide a model for the conduct of similar baseline studies.

C. S. Hickman

Manuscripts

Manuscripts must be typed on white paper, 8½" by 11", and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e.*, not justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

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b) Books

Yonge, C. M. & T. E. Thompson. 1976. Living marine molluscs. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117-135. *In*: R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, Calif.

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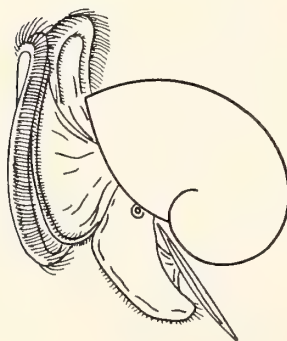
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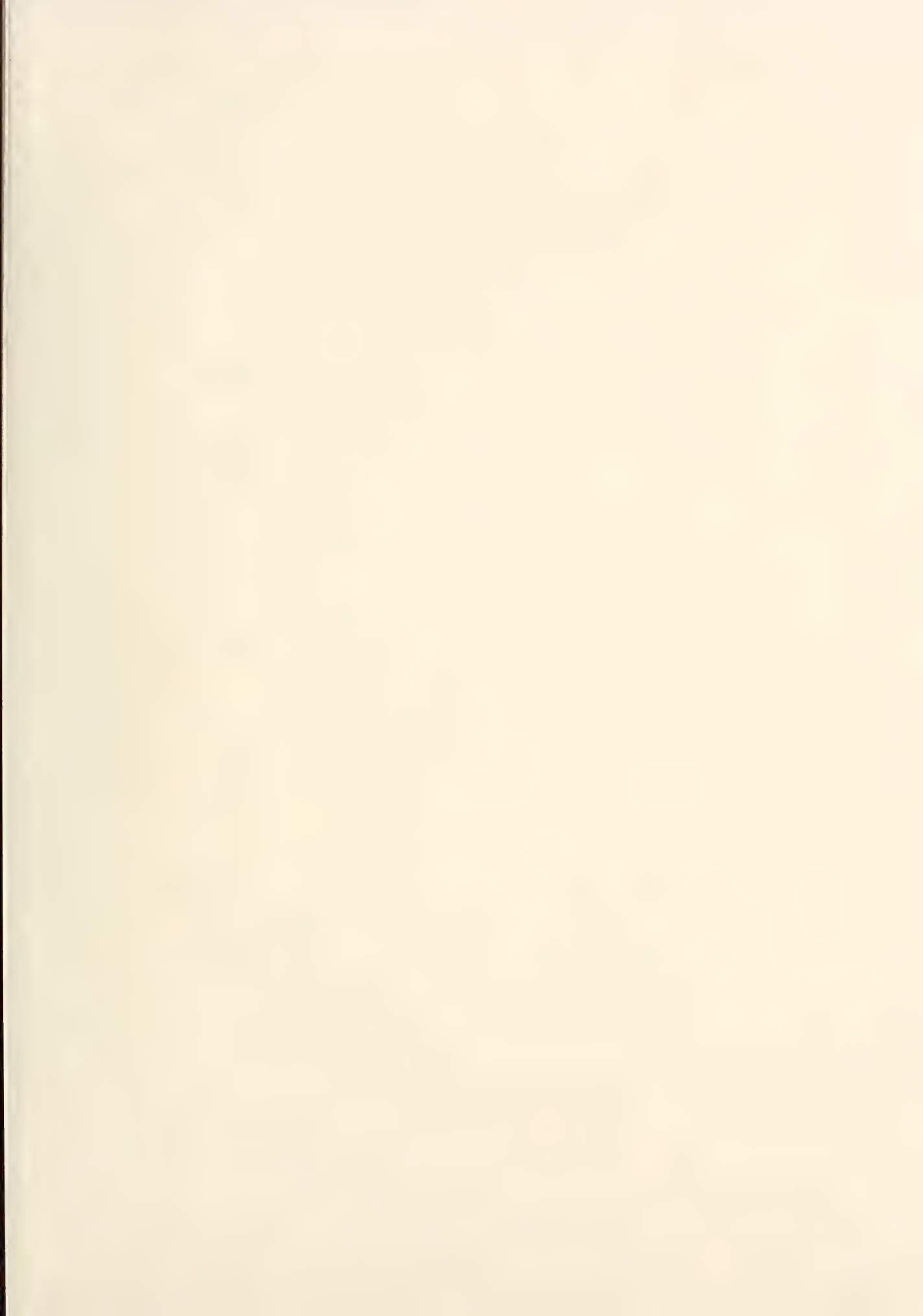
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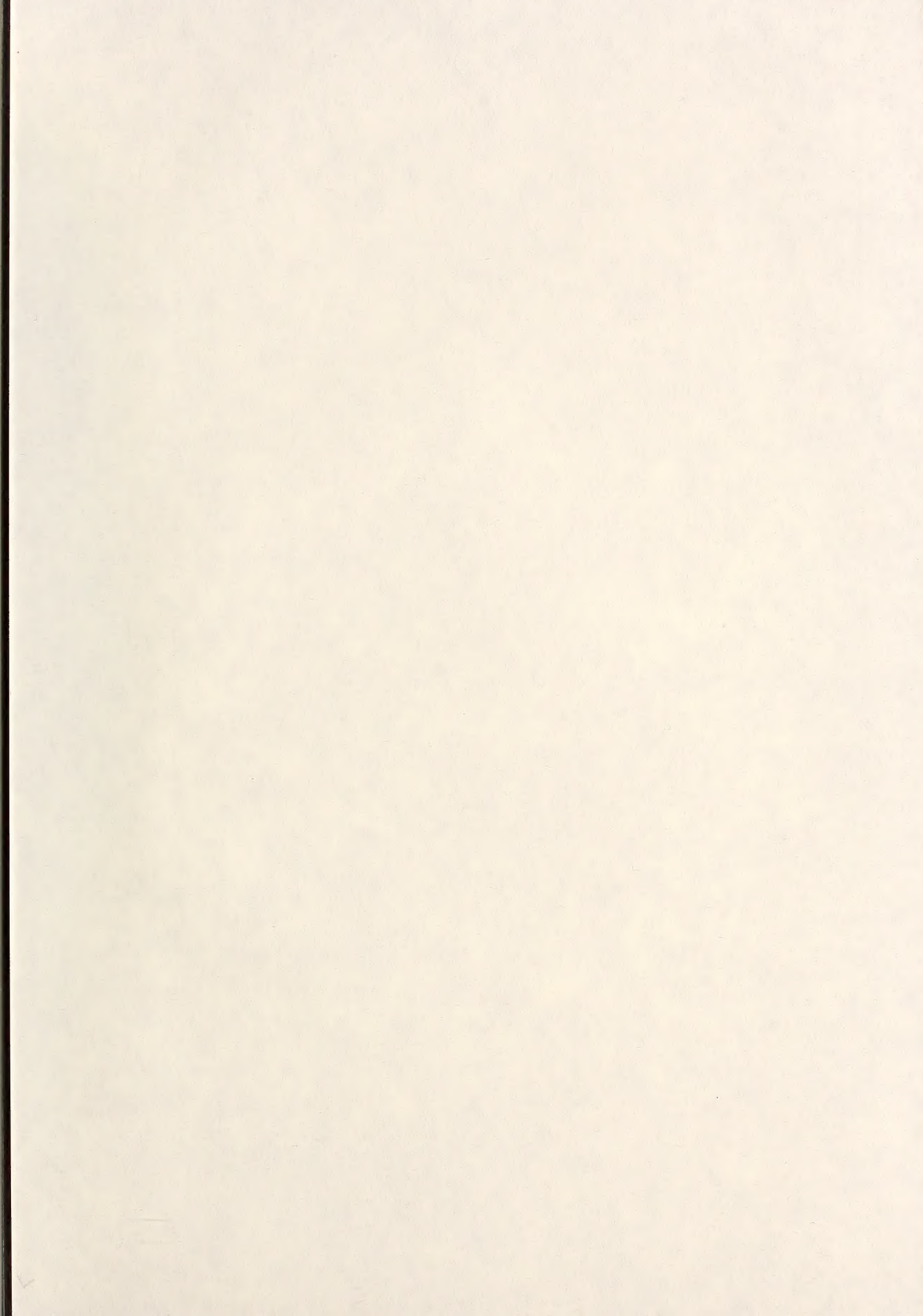
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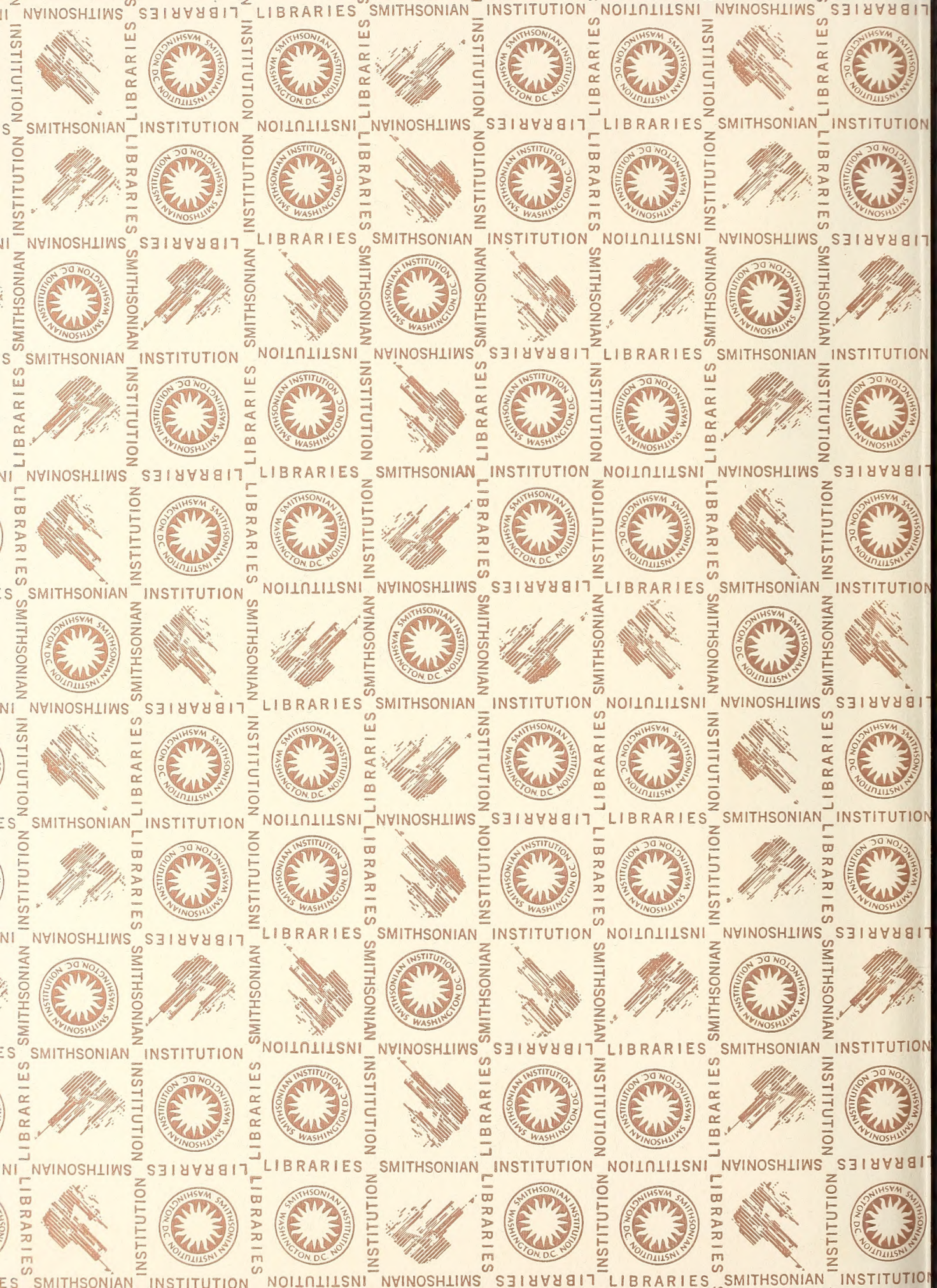
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